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MATHEMATICS.—*Experiments in the solution of differential equations by Monte Carlo methods.*

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[*Dedicated to* DR. LYMAN J. BRIGGS *on his eightieth birthday*]

INTRODUCTION

We propose to discuss certain experiments on the solution of

$$\frac{\partial^2 V}{\partial x^2} + \frac{\partial^2 V}{\partial y^2} = 0 \tag{1}$$

for $0 < x < 1$, $0 < y < 1$ with boundary conditions

$$\begin{aligned} V(x, 1) &= \sin \pi x, \; V(x, 0) = 0, \\ &\qquad 0 < x < 1, \\ V(0, y) &= 0, \; V(1, y) = 0, \\ &\qquad 0 < y < 1 \end{aligned} \tag{2}$$

by the computational method known by the name of Monte Carlo, using SEAC, the National Bureau of Standards Eastern Automatic Computer. This simple example was chosen because the exact solution to it and to an approximating difference equation are known ((5), (6) below).

Accounts of the basic principles of the Monte Carlo method have been given, for instance, by Curtiss [2] and in recent textbooks for numerical analysis. A comprehensive report is in preparation by H. Kahn and A. W. Marshall.

[1] Some of this material was presented to the Association for Computing Machinery, Washington, D. C., September 7–9, 1950; some to a conference on Fluid Mechanics, Cambridge, Mass., September 1950, and some to the Institute of Mathematical Statistics, Boston, Mass., December 26, 1951.

Much of the coding and machine operation was carried out by Viola D. Hovsepian. Most of the material summarized or mentioned here is accessible in the files of the National Bureau of Standards' Computation Laboratory.

The basic facts about SEAC are these: It is a general purpose computer now having 1,024 words[2] of high-speed memory (mercury delay line and Williams tubes) and about 100,000 of intermediate memory (magnetic tape). The time for multiplication is about 3 milliseconds and for addition about 1 millisecond. More detailed descriptions have been given by Greenwald et al. [10].

EXACT SOLUTION

The Monte Carlo method provides a statistical estimate to the solution, not of the differential equation (1), but of an approximating difference equation, which we shall now discuss. Consider a lattice with square meshes of side $h = 1/(l + 1)$ for an integral value of l; write

$$u(mh, nh) = u(m, n).$$

Then consider the difference equation

$$\begin{aligned} &u(m - 1, n) + u(m, n - 1) - 4u(m, n) \\ &\quad + u(m, n + 1) + u(m + 1, n) = 0 \end{aligned} \tag{3}$$

for $m, n = 1, 2, \cdots, l$ with boundary conditions

$$\begin{aligned} u(m, l + 1) &= \sin \pi mh, \quad u(m, 0) = 0, \\ &\qquad m = 0, 1, 2, \cdots, l + 1 \\ u(0, n) &= 0, \quad u(l + 1, n) = 0, \\ &\qquad n = 0, 1, 2, \cdots, l + 1 \end{aligned} \tag{4}$$

The difference $|u - V|$ can be estimated e.g., in terms of the derivatives of the boundary functions (2). [See for instance W. Wasow [6], P. C. Rosenbloom [4], J. L.

[2] A word consists of 45 binary digits.

Walsh and D. M. Young [5]]. In our case this is unnecessary for the solution to (4) is known to be:

$$(5) \quad u(m, n) = \sin \pi m h \sinh \lambda \pi n h / \sinh \lambda \pi$$

where λ is defined by

$$\sinh \tfrac{1}{2} \lambda \pi h = \sin \tfrac{1}{2} \pi h.$$

In most of our experiments l was taken to be 15; this gives $\lambda \doteq .9968$.

The exact solution of the differential equation (1) is

$$(6) \qquad V = \frac{\sin \pi x \sinh \pi y}{\sinh \pi}.$$

THE MONTE CARLO PROCESS[3]

Consider the following problem. A particle begins at an interior point $P = P_0$ of the lattice and continues in the following way: if at any time it is at $P = (\alpha, \beta)$ then it moves to one of the neighboring points $(\alpha, \beta - h)$, $(\alpha - h, \beta)$, $(\alpha + h, \beta)$, $(\alpha, \beta + h)$ and the probability of moving to any one of these is 1/4. When it reaches a point Q on the boundary then the walk is terminated and the value $u(Q)$ is scored. The process is then repeated by starting a new walk at P. The problem is: what is the expected value of the score?

It has been shown (see, for instance, Curtiss [2, §9]) that the expected value of the score is the solution $u(P)$ to the difference equation (3) subject to the boundary conditions (4).

In practice this expected value is estimated as the arithmetic mean of the scores obtained by a number of walks. The dispersion of this mean has been examined by Curtiss [2, §14]. He shows that in order to obtain m correct decimal places in $u(P)$ it is necessary to take about 4×10^{2m} walks in the case under discussion. A more sophisticated approach which can cut down the amount of computing required is discussed in §8 below.

COMPUTATIONAL PROCESS

The actual computations are readily carried out. We used the pseudo-random numbers $\{\rho_n\}$ generated by the relation

$$\rho_n = 2^{-42} \nu_n; \nu_{n+1} = \nu \nu_n \pmod{2^{42}},$$
$$\nu_0 = 1, \nu = 5^{17}.$$

The quality of these numbers is discussed by Cameron et al [1]; see also Taussky and Todd [1a]. We determined the direction of the n-th step by finding out which of the inequalities

$$0 \leqq \rho_n < \tfrac{1}{4}, \tfrac{1}{4} \leqq \rho_n < \tfrac{1}{2}, \tfrac{1}{2} \leqq \rho_n < \tfrac{3}{4}, \tfrac{3}{4} \leqq \rho_n \leqq 1$$

were satisfied and moving north, west, south or east accordingly. After carrying out each new step it is necessary to decide whether or not the boundary is reached; in the first case we have to add the boundary value $u(Q)$ to the running total and return and begin a new walk, while in the second we have to take a new step.

The programs used were arranged to display various items of information. For instance, in one of the programs, the following was printed out after every 64 walks. (Note that the last four entries are in the hexadecimal notation.)

average of u	3216905334
average of u^2	2720643477
total number of steps	136D
total number of walks	40
number of excessively long walks	0
current random number	3C95C737C11

Each such run of 64 walks took about 30 seconds on the machine, of which 12 seconds was consumed in printing.[4]

A few remarks are necessary in explanation of the fifth entry. Theoretically the probability of a walk of infinite length is zero and so such walks do not contribute to the expected value of u. In practice, with pseudorandom numbers, it is conceivable, for instance, that the path should become cyclic, never reaching the boundary, so that the computation would never proceed significantly. To prevent this a tally of the number of steps in each walk was kept: if this exceeded a chosen constant (in most of our cases 1,024) the walk was stopped.

[3] A description of this process in terms of diffusion has been given by McCrea and Whipple [3].

[4] This very frequent print-out was the practice when these experiments were carried out (summer 1950) when SEAC was still in its infancy. At present prints-out in similar circumstances would be made every 15 or 30 minutes.

The printing of this material enabled the computation to be easily carried further, after a voluntary or involuntary stop.

We note here that an estimate of the time for a computation can be based on an allowance of 5 milliseconds for each step of the walk and use of the results of Curtiss [2, §9] and Wasow [7, 8].

SUMMARY OF MAIN RESULTS

Experiments were carried out to evaluate u at the points P_1: $(\frac{1}{2}, \frac{1}{2})$, P_2: $(\frac{3}{4}, \frac{3}{4})$, P_3: $(\frac{3}{4}, \frac{1}{4})$ and P_4: $(\frac{7}{8}, \frac{1}{2})$. The results obtained are shown below. The solutions to the differential equation and to the difference equation were computed from (5) and (6).

TABLE 1

$x = \frac{1}{2}, y = \frac{1}{2}$:	differential equation	.1993
	difference equation	.2002
	Monte Carlo 6,592 walks	.2014
$x = \frac{3}{4}, y = \frac{3}{4}$:	differential equation	.3201
	difference equation	.3209
	Monte Carlo 2,176 walks	.3001
$x = \frac{3}{4}, y = \frac{1}{4}$:	differential equation	.0532
	difference equation	.0534
	Monte Carlo 13,440 walks	.0530
$x = \frac{7}{8}, y = \frac{1}{2}$:	differential equation	.0763
	difference equation	.0766
	Monte Carlo 10,368 walks	.0807

The varying number of walks used was accidental—in some cases, for instance, the experiment was stopped when a machine failure occurred. For the sake of comparison we give in Table 2 the successive estimates of $10^4\ u$, after each run of 64 walks. Three experiments were carried out on the first point and the results are given in the columns labeled $P_1(1)$, $P_1(2)$, $P_1(3)$; the value quoted above is that got by pooling the results of all the runs.

The results obtained from experiments on P_2 are given in Column P_2. More extensive experiments were carried out on P_3 and P_4; the early results are given in the columns labeled P_3 and P_4 in Table 2.

TABLE 2

$P_1(1)$	$P_1(2)$	$P_1(3)$	P_2	P_3	P_4	P_1
1362	3217	2309	2574	0060	1127	1935
1391	2246	1769	2807	0190	0987	1691
1697	1900	1852	2887	0243	0823	1899
1580	1886	1938	2985	0215	0733	1790
1668	1878	1935	3077	0338	0681	1729
1756	1958	1874	2985	0332	0809	1818
1779	2019	1887	3051	0343	0765	1820
1754	2115	1858	2938	0341	0740	1879
1777	2067	1804	2926	0319	0775	1869
1764	2067	1786	2965	0344	0740	1828
1729	2102	1744	2974	0343	0733	1825
1720	2089	1739	3020	0327	0729	1818
1690	2063	1804	2955	0363	0732	1793
1689	2103	1804	2977	0377	0729	1800
1749	2090	1811	2948	0409	0766	1802
1752	2037	1838	2945	0383	0803	1801
1762	2039	1861	2937	0373	0835	1818
1789	2055	1861	2916	0370	0816	1827
1812	2105	1898	2905	0362	0828	1829
1814	2116	1927	2919	0363	0797	1851
1850	2113	1953	2930	0350	0789	1888
1878	2094	1937	2911	0361	0791	1881
1904	2095	1942	2884	0373	0786	1887
1891	2071	1932	2937	0366	0782	1889
1898	2107	1954	2955	0380	0784	1890
1890	2105	1923	2945	0383	0763	1922
1912	2110	1923	2940	0384	0771	1896
1885	2137	1934	2955	0379	0763	1886
1886	2149	1978	2972	0397	0768	1899
	2116	1954	2963	0397	0768	1930
	2132	1930	2991	0398	0763	1926
	2127	1928	2994	0407	0760	1913
	2151	1925	2984	0408	0768	1918
	2158	1938	3001	0421	0768	1909
	2146	1951		0432	0771	1900
	2151	1974		0429	0762	1906
	2154			0429	0763	1929
	2149			0433	0776	1916
				0428	0771	1916
				0427	0773	1933
				0423	0788	1936
				0432	0789	1936
				0428	0788	
				0440	0799	
				0435	0805	
				0425	0798	
				0425	0805	
				0426	0799	
				0432	0794	
				0432	0791	

VARIANCE OF ESTIMATES

It is possible to find the theoretical variance of u. An expression for the probability $p(P, Q)$ of a walk starting at a particular interior point P and ending at a particular boundary point Q has been given by McCrea and Whipple [3]. We can then evaluate

$$\sigma^2(P) = \sum_Q (u(Q) - u(P))^2 p(P, Q).$$

This has been done in the case of P_1 and P_2 and we found

$$\sigma(P_1) = .319,$$
$$\sigma(P_2) = .206.$$

The values for the theoretical standard deviation of means corresponding to runs of 64 walks are obtained by division by 8 and are

$$\sigma_{64}(P_1) = .040,$$
$$\sigma_{64}(P_2) = .026.$$

The results of the second and third experiments from P_1 (i.e., columns of Table 2) have been investigated further. The means of the individual runs of 64 walks were obtained from the accumulated means recorded in Table 2; these are given on Table 3 below, each entry has been multiplied by 10^5. From these we found the observed values of σ_{64} to be .046 and .045, which compare with the theoretical value of .040. It will be noted that all the entries lie within $3\sigma_{64}$ of the mean.

TABLE 3

Second experiment (column $P_1(2)$ of Table 2)

32169	12751	12077	18439	18464	23580
23836	27916	16780	20638	24526	19540
17474	26244	19036	12434	20777	23291
29902	23366	20511	16951	21102	15164
29682	20650	22454	28522	24934	11650
25967	19909	28962	23988	17309	23401
22658	19566				

Third experiment (column $P_1(3)$ of Table 2)

23095	12285	20171	21965	19209	15733
19632	16526	13726	16278	13220	16852
25880	17946	19207	22403	22259	18665
25663	24625	24831	15901	20654	16974
24770	11478	19228	22224	32182	12758
12073	18439	18451	23569	23858	27894

DURATION OF WALKS

Wasow [7, 8] has studied the duration of random walks theoretically. He obtained expressions for the mean $\bar{N}$ and the variance σ^2 of the duration which are valid asymptotically as the length of the steps tends to zero. Explicit results are obtained for walks in an n-dimensional sphere, and bounds in the case of other regions, in particular the n-dimensional cube.

In the present case, an upper bound for the expected length $\bar{N}$ is 81; in the first of the experiments on P_1 the average length turned out to be 75; the total number of steps in runs of 64 consecutive walks in this experiment were:

4757	5369	4154	4693	4675	4442
4942	4886	4479	4435	5023	4556
4715	4856	5450	4714	4700	4931
4857	4160	4767	5241	5776	4642
4527	4646	5719	4400	4681	

An estimate for a "relative error": $\sigma/\bar{N}$ in the present case is .7071, giving $\sigma \doteq 57$.

IMPORTANCE SAMPLING

The application to Monte Carlo problems of the technique known as importance sampling or as sampling with probability in proportion to size, was suggested by Kahn (see e.g. Curtiss [2, §16]). Theoretically this can lead to zero-variance estimates. Practically, it appears attractive in so far as it can make use of known approximations to the solution of the equation under investigation.

Let us suppose that an approximation v^* to the solution V of (1) is known. Then the process consists in using a walk biassed towards points with larger values of v^* which is however, compensated by a weighting. In particular we define

$$p_i = \frac{v^*(R_i)}{v^*(R_1) + v^*(R_2) + v^*(R_3) + v^*(R_4)} \qquad (i = 1, 2, 3, 4)$$

where R_1, R_2, R_3, R_4 are the points of the lattice which are north, west, south and east of P. The step from P is to the points P_i with probability p_i. This is carried out by deciding in which of the intervals

$$[0, p_1], [p_1, p_1 + p_2], [p_1 + p_2, p_1 + p_2 + p_3], [p_1 + p_2 + p_3, 1]$$

the current random number lies. After this step, say to R_j, the current weight of the particle is multiplied by $(4\ p_j)^{-1}$. A new step is now taken from R_j, with new biasses. Whenever the boundary is reached at Q say, the modified weight of the particle is multiplied by $v(Q)$ to give the score for this walk. It can be shown that the expected value of the score is again $u(P)$. Moreover, if $v^* = u$, this has zero-variance. It is therefore to be expected that the use of an approximation v^* would lead to estimates with small variance.

The following experiment was carried out. We took

$$v^* = 2xy,\ 0 < x < \tfrac{1}{2},\ 0 < y < 1$$
$$v^* = 2(1 - x)y,\ \tfrac{1}{2} < x < 1,\ 0 < y < 1.$$

The results of 42 runs of 64 walks beginning at $(\frac{1}{2}, \frac{1}{2})$ are shown in the column labelled P_1 in Table 2.

We note that the computations in this case are considerably more extensive than in the straightforward case. We have to compute v^* at three new points after each step, and then compute the p_i ; the choice having been made we require another division to account for the weight. In the actual experiment, it was found that it took about 5 minutes to carry out a run of 64 walks compared to 20 seconds required in the simple case. More elaborate approximations would presumably require more time; alternatively it would be possible to replace this loss of time by a loss of space, storing the values of v^* in the high-speed memory or in the auxiliary memory of the machine. We have not yet examined these points in detail. However, that the use of importance sampling does not seem to be of great advantage in the present circumstances is evident by comparison of the results given in the last column of Table 2 with those of the first three.

CONCLUSION

It is clear that the Monte Carlo method is not an economical one in the present case. A single computer experienced in relaxation techniques would be able to obtain results of comparable accuracy in comparable time. However, the difficulty of handling similar problems in higher dimensions manually increases exceedingly rapidly. Experiments on problems exactly analogous to (1, 2) in 3, 5, 16 dimensions have been carried out on SEAC by C. J. Swift and M. Tikson; it is found, as expected, that results of comparable accuracy are obtained without a great increase in effort.

For clarity we state the problem in the case of 3-dimensions. It is to solve

$$\frac{\partial^2 V}{\partial x^2} + \frac{\partial^2 V}{\partial y^2} + \frac{\partial^2 V}{\partial z^2} = 0$$

for $0 < x < 1$, $0 < y < 1$, $0 < z < 1$ subject to V vanishing on all faces of the cube except the one where $z = 1$ where $V(x, y, 1) = \sin \pi x \sin \pi y$ for $0 \leqslant x \leqslant 1$, $0 \leqslant y \leqslant 1$.

The solution to this problem is

$$V = \sin \pi x \sin \pi y \frac{\sinh \pi\sqrt{2}z}{\sinh \pi\sqrt{2}}.$$

There follows some results of experiments to determine the value of V at the centers of the cubes:

3-dimensions	
differential equation	.1072
difference equation	.1083
Monte Carlo, 23000 walks	.1097
mean length of walk	86
5-dimensions	
differential equation	.0422
difference equation	.0442
Monte Carlo, 2880 walks	.0468
mean length of walk	106
16-dimensions	
differential equation	.00228
difference equation	.00264
Monte Carlo, 2176 walks	.00296
mean length of walk	201

REFERENCES

[1] CAMERON, J. M., NEWMAN, M., TAUSSKY, O. and TODD, JOHN. *The generation and testing of pseudo-random numbers on SEAC.* To appear.

[1a] TAUSSKY, O. and TODD, JOHN. *The generation and testing of pseudo-random numbers.* Proceedings of a Symposium on Monte Carlo Methods, March 16–17, 1954, Gainesville, Fla. To appear.

[2] CURTISS, J. H. *Sampling methods applied to differential and difference equations.* Seminar on Scientific Computation, International Business Machines Corporation, 1949.

[3] MCCREA, W. H. and WHIPPLE, F. J. W. *Random paths in two and three dimensions.* Proc. Royal Soc. Edinburgh **60:** 281–298. 1940.

[4] ROSENBLOOM, P. C. *The difference equation method for solving the Dirichlet problem.* In Construction and Applications of Conformal Maps, NBS Applied Math. Series, **18:** 231–237. 1953.

[5] WALSH, J. L. and YOUNG, D. M. *On the accuracy of the numerical solution of the Dirichlet problem by finite differences.* NBS Journ. Res. **51:** 343–363. 1953.

[6] WASOW, W. *On the truncation error in the solution of Laplace's equation by finite differences.* NBS Journ. Res. **48:** 345–348. 1952.

[7] ———. *On the duration of random walks.* Ann. Math. Stat. **22:** 199–216. 1951.

[8] ———. *On the mean duration of random walks,* NBS Journ. Res. **46:** 462–471. 1951.

[9] ———. *Random walks and the eigenvalues of elliptic differential equations.* NBS Journ. Res. **46:** 65–73. 1951.

[10] GREENWALD, S., HAUETER, R. C. and ALEXANDER, S. N. SEAC. Proc. I.R.E. **41:** 1300–1313. 1953.

MATHEMATICS.—*A representation for solutions of analytic systems of linear differential equations.*[1] H. A. ANTOSIEWICZ, American University, and MILTON ABRAMOWITZ, National Bureau of Standards.

[*Dedicated to* DR. LYMAN J. BRIGGS *on his eightieth birthday*]

1. *Introduction.*—Linear ordinary differential equations with analytic coefficients that depend continuously upon some parameters are of great importance in applied mathematics where they frequently arise, for instance, in the solution of linear partial differential equations by Bernoulli's method of separation of variables. It is often desired to describe the behavior of the solutions of such an equation, for certain ranges of the parameters involved, in terms of the solution of a related differential equation which, in some sense, approximates the particular equation studied. A case of special interest is that when the characteristic equation has for some value of the independent variable an isolated multiple root which is equal to zero, i.e., when the behavior of the solution is to be determined in the so-called transition region. The equation $d^2x/dt^2 + t^\alpha x = 0$, $\alpha > 0$, in the neighborhood of $t = 0$, serves as simple illustration for this situation; it arises in the study of linear heat flow along a slender rod with variable thermal conductivity.

In this note we consider an n-dimensional vector differential equation

$$\frac{dx}{dt} = A(t, z)x \tag{1}$$

where $A(t, z)$ is analytic in the scalar variable t and continuous in the k-dimensional vector parameter z for all $|t| \leqq \tau < \infty$ and $\|z\| \geqq \zeta \geqq 0$,[2] being representable in a convergent series

$$A(t, z) = \sum_0^\infty A_i(z)t^{i+\nu} \tag{2}$$

where $A_0(z) \not\equiv 0$ and ν is some positive integer or zero. Let

$$\frac{dy}{dt} = B(t)y \tag{3}$$

be another n-dimensional vector differential equation with $B(t)$ analytic in t for $|t| \leqq \tau < \infty$,

$$B(t) = \sum_0^\infty B_i t^{i+\nu}, \qquad B_0 \neq 0, \tag{4}$$

whose general solution

$$y(t) = Y(t)c \tag{5}$$

is assumed to be known. This suggests the question of whether the general solution of (1) may be expressed in the form

$$x(t, x) = X(t, z)\ Y(t)c \tag{6}$$

where $X(t, z)$ is suitable determined. We shall prove that the answer is in the affirmative.

Problems of this kind arise in applied mathematics where equation (3) is frequently a "limiting" equation of (1); i.e. $B(t)$ may be, for example, the limit of $A(t, z)$ as $\|z\| \to \infty$. A few illustrations, of interest in applied work, are given at the end.

2. *Theorem.—The general solution of* (1) *may be represented in the form*

$$x(t, z) = X(t, z)\ Y(t)c$$

where $X(t, z)$ *is analytic in* t *and continuous in* z *for* $|t| < \sigma < \tau$ *and* $\|z\| \geqq \zeta \geqq 0$.

Proof. Substituting (6) into (1) and using (3), we obtain $[X' + (XB(t) - A(t, z)X)]Y(t)c = 0$; thus (6) will be a solution of (1) if $X(t, z)$ is a solution of the matrix equation

$$X' + XB(t) - A(t, z)X = 0. \tag{7}$$

Assuming a formal expansion

$$X(t, z) = \sum_0^\infty X_i(z)t^i \tag{8}$$

and using (2) and (4) we find that (7) is satisfied if

[1] This work was supported (in part) by the Office of Naval Research.

[2] The norm $\|v\|$ of a vector $v = (v_i)$ is defined as $\|v\| = \Sigma_i |v_i|$; the norm $\|M\|$ of a matrix $M = (m_{ij})$ as $\|M\| = \Sigma_{ij} |m_{ij}|$.

$$(9)\quad X_i(z) = \begin{cases} 0, & 1 \leqq i \leqq \nu \\ \dfrac{-1}{i}\displaystyle\sum_{j=0}^{i-\nu-1} (X_{i-j-\nu-1}B_j - A_j(z)X_{i-j-\nu-1}), & i \leqq \nu+1. \end{cases}$$

Since $X_0(z)$ is arbitrary, we take $X_0(z) = I$. To complete the proof[3] observe that from the hypotheses on (1) and (3) it follows that $\| A(t, z) \| \leqq \alpha(z)$ for $|t| \leqq \tau$ and every z with $\| z \| \geqq \zeta \geqq 0$ and $\| B(t) \| \leqq \beta$ for $|t| \leqq \tau$; hence $\| A_i(z) \| \leqq \alpha(z)\ \tau^{-i-\nu}$, $\| B_i \| \leqq \beta\tau^{-i-\nu}$, [1]. Let $\sigma = \theta\tau$, $0 < \theta < 1$; let i_0 be some integer, $i_0 \geqq \tau(\alpha(z) + \beta)(1 - \theta)^{-1}$, and $\xi(\tau, z) = \max\{\sigma^i \| X_i(z) \|\}$ for $0 \leqq i \leqq i_0$. Then

$$(10)\quad \| X_i(z) \| \leqq \xi(\tau, z)\sigma^{-i}, 0 < \sigma < \tau,$$

is true for $0 \leqq i \leqq i_0$. Assuming (10) holds for some $i > i_0$, we find from (9)

$$\sigma^{i+1} \| X_{i+1}(z) \| \leqq \frac{\tau}{i+1}\sum_0^{i-\nu} \theta^{1+j+\nu}\sigma^{i-j-\nu} \cdot \| X_{i-j-\nu} \| \{\tau^{j+\nu}(\| B_j \| + \| A_j(z) \|)\}$$

$$\leqq \tau(\alpha(z) + \beta)\xi(\tau, z)(i+1)^{-1}\sum_0^{i-\nu}\theta^{1+j+\nu}$$

$$(11)\quad \leqq \tau(\alpha(z) + \beta)\xi(\tau, z)(i_0 + 1)^{-1}(1 - \theta)^{-1}$$

$$\leqq \xi(\tau, z).$$

Hence, by induction, (10) is true for all $i \geqq 0$.

It follows that for all $|t| < \sigma < \tau$, $\| z \| \geqq \zeta \geqq 0$,

$$(12)\quad \sum X_i(z)t^i << \xi(\tau, z) \sum (t/\sigma)^i$$

and thus $X(t, z)$ is analytic in t for $|t| < \sigma < \tau$ and continuous in z for $\| z \| \geqq \zeta \geqq 0$.

3. *Examples.*—(*i*) The Coulomb Wave functions $F_0(\eta, \rho)$, $G_0(\eta, \rho)$ are linearly independent solutions of the equation

$$\frac{d^2x}{d\rho^2} + \left(1 - \frac{2\eta}{\rho}\right)x = 0, \qquad \eta > 0.$$

Letting

$$t = \frac{2\eta - \rho}{(2\eta)^{1/3}}, \qquad z = (2\eta)^{2/3}$$

this equation is transformed into the equation

$$(1a)\qquad \frac{d^2x}{dt^2} - \frac{zt}{z - t}x = 0.$$

Its "limiting" equation as $z \to \infty$ is

$$(3a)\qquad \frac{d^2y}{dt^2} - ty = 0$$

whose general solution may be written in the form

$$(5a)\quad y(t) = c_1Ai(t) + c_2Bi(t)$$

where $Ai(t)$, $Bi(t)$ are the Airy integrals, which are defined for $t \geqq 0$ as

$$Ai(t) = 1/3\ \sqrt{t}\{I_{-1/3}(2/3\ t^{3/2}) - I_{1/3}(2/3\ t^{3/2})\},$$

$$Bi(t) = \sqrt{t/3}\{I_{-1/3}(2/3\ t^{3/2}) + I_{1/3}(2/3\ t^{3/2})\}.$$

Our theorem yields for the general solution of (1*a*) the representation

$$(6a)\quad x(t, z) = \phi(t, z)\ y(t) + \psi(t, z)\ dy(t)/dt$$

where the functions $\phi(t, z)$, $\psi(t, z)$ are analytic in t for $|t| < z$, being expressible in convergent series

$$\phi(t, z) = \sum_0^\infty a_i(z)t^i \equiv 1 + \frac{1}{12z}t^4 + \frac{1}{20z^2}t^5 + \cdots$$

$$\psi(t, z) = \sum_0^\infty b_i(z)t^i \equiv -\frac{1}{30z}t^5 - \frac{1}{60z^2}t^6 - \cdots$$

where

$$a_0 = 1,\ a_1 = a_2 = a_3 = 0,$$

$$b_0 = b_1 = b_2 = b_3 = 0,$$

$$a_{i+4} = \frac{1}{(i+3)(i+4)} \cdot \left\{\sum_0^i z^{-j-1}a_{i-j} - (2i+5)b_{i+2}\right\},$$

[3] Cf., for example, [2].

(9a) $i \geqq 0$

$$b_{i+4} = \frac{1}{(i+3)(i+4)} \cdot \left\{ \sum_{0}^{i} z^{-j-1} b_{i-j} - (2i+6) a_{i+3} \right\}.$$

(*ii*) Consider the equation for parabolic cylinder functions

(1b) $$\frac{d^2x}{dt^2} - \left(z + \frac{t^2}{4}\right)x = 0, \quad |z| \leqq \zeta < \infty,$$

and its "limiting" equation as $z \to 0$,

$$\frac{d^2y}{dt^2} - \frac{t^2}{4}\, y = 0$$

whose general solution is

(5b) $$y(t) = t\left\{ c_1 I_{1/4}\left(\frac{t^2}{4}\right) + c_2 I_{-1/4}\left(\frac{t^2}{4}\right)\right\}.$$

Our theorem furnishes the representation

(6b) $x(t, z) = f(t, z)y(t) + g(t, z)dy(t)/dt$

where the functions $f(t, z)$, $g(t, z)$ are analytic in t for all t, being expressible in the form

(8b) $$f(t, z) = \sum \alpha_i(z) t^i \equiv 1 + (z/2)t^2 + \cdots$$
$$g(t, z) = \sum \beta_i(z) t^i \equiv (z/3)t^3 + \cdots$$

where

$$\alpha_0 = 1, \ \alpha_1 = 0, \ \alpha_2 = z/2,$$
$$\beta_0 = \beta_1 = \beta_2 = 0,$$
$$\alpha_{i+1} = \frac{1}{(i+1)(i+2)} \cdot [z\alpha_i - (i/2)\beta_{i-1}],$$

(9b)

$$\beta_{i+2} = \frac{1}{(i+1)(i+2)} \cdot [z\beta_i - 2(i+1)\alpha_{i+1}].$$

REFERENCES

[1] PICARD, EMILE. *Traité d'analyse* **2** (chap. 9). Paris, 1905.

[2] LEFSCHETZ, S. *Lectures on differential equations*: 35. Princeton, 1948.

PALEONTOLOGY.—*New names for two foraminiferal homonyms.* ALFRED R. LOEBLICH, JR., and HELEN TAPPAN, U. S. National Museum.

Two species discussed in our recent publication *Studies of Arctic Foraminifera* are or have homonyms, as was kindly brought to our attention by Dr. Hans Thalmann. On page 68 the allocation of *Entosolenia costata* Williamson (1858, p. 9) to the genus *Oolina* places it as a homonym of *Oolina costata* Egger (1857, p. 269) from the Miocene of Bavaria. We therefore propose *Oolina borealis*, new name, for *Entosolenia costata* Williamson, 1858 (not *Oolina costata* Egger, 1857).

Furthermore, the allocation (p. 77) of *Vermiculum marginatum* Montagu (1803, p. 524) to *Fissurina* places as a homonym the species *Fissurina* (*Fissurine*) *marginata* Seguenza (1862, p. 66) from the upper Miocene of Messina, Sicily. For the species of Seguenza we are therefore proposing *Fissurina siciliensis*, new name.

EGGER, J. G. *Die Foraminiferen der Miocän—Schichten bei Ortenburg in Nieder-Bayern.* Neues Jahrb. Min. Geogn. Geol. Petref.-Kunde 1857: 266–311, pls. 5–15.

LOEBLICH, ALFRED R., JR., and TAPPAN, HELEN. *Studies of Arctic Foraminifera.* Smithsonian Misc. Coll. **121** (7), 1–150, pls. 1–24. 1953.

MONTAGU, G. *Testacea Britannica, or natural history of British shells marine, land and fresh water, including the most minute:* 1–606, pls. 1–16. 1803.

SEGUENZA, G. *Dei terreni Terziarii del distretto di Messina; Parte II—Descrizione dei foraminiferi montalamici delle marne mioceniche del distretto di Messina:* 84 pp., 2 pls. 1862.

WILLIAMSON, W. C. *On the Recent Foraminifera of Great Britain:* 1–107, pls 1–7. Ray Society, London, 1858.

BOTANY.—*Some more notes on United States ashes* (Fraxinus). WILLIAM A. DAYTON, U. S. Forest Service.

It is widely agreed that the taxonomic (and hence nomenclatural) status of some of our United States tree genera is still not quite satisfactory; represented among these genera are oaks, hickories, basswoods (lindens), and ashes.

Shortly after Dr. Little's paper *Notes on* Fraxinus (*ash*) *in the United States* (this JOURNAL **42:** 369–380. Dec. 1952) appeared, he left for a year's assignment in Venezuela, and most of the correspondence about it was routed to me. Many voiced their disappointment that a key was not included in the paper.

The purpose of these notes is (1) to provide a preliminary key as a mark for others to shoot at and (2) to make some observations on Lamarck's American ash types.

Probably the most popular sectional and subsectional organization of *Fraxinus* in this country is that shown by Rehder (*Manual of Cultivated Trees and Shrubs Hardy in North America*. Ed. 2. 1940) from which the following key is adapted:

Flowers appearing with or after the leaves, perfect or polygamous, in terminal and lateral panicles.....Sec. ORNUS
Corolla present; scales of terminal bud entire. Subsec. *Euornus*
Corolla absent; outer scales of terminal bud foliar.....Subsec. *Ornaster*
Flowers appearing before the leaves, usually apetalous, in lateral panicles Sec. FRAXINASTER
Flowers with (2) petals....Subsec. *Dipetalae*
Flowers without petals.
Flowers with calyx.
Leaflets small, rachis winged Subsec. *Sciadanthus*
Leaflets large, rachis unwinged Subsec. *Melioides*
Flowers without calyx Subsec. *Bumelioides*

Our native United States ashes belong to all six subsections, except *Ornaster* and especially to *Melioides*. It will be observed that the above key (and most ash keys for that matter) places great emphasis on flowers, evanescent characters which, though highly important taxonomically, tend to discourage the average person trying to identify ashes. Fruits are next in importance in the average ash key, and these parts too are naturally often lacking, especially in a genus frequently dioecious. With the object of attempting to emphasize "field" and vegetative characters as much as possible the following preliminary key is offered. The nomenclature follows Little's treatment (*op. cit.*) and in *Check list of native and naturalized trees of the United States, including Alaska* (U. S. Dept. Agr. Handb. 41. 1953).

KEY TO UNITED STATES ASH SPECIES

1. Twigs 4-sided. Samaras more or less flattened, with wing extending to base.
2. Eastern species; leaflets 7–11; upland timber-size tree. *Additional characters*: Twigs acutely 4-angled, when crushed will turn fresh-water blue—a dyestuff of the pioneers; buds gray; perfect flowers only; fruits not persistent. Wood heavy, hard, rather brittle. *F. quadrangulata* Michx. (blue ash)
2. Western species; leaflets 1–9; small trees or shrubby.
3. Californian species; leaflets stalked, usually 5, glabrous; corolla present, 2-petaled. Foothill slopes, mostly shrubby, showy in bloom
F. dipetala Hook. & Arn. (two-petal ash)
3. Southwestern species (w. Colo.-s. Utah-s. Nev.-n. Ariz.-n. N. Mex. In Calif. rare and only on e. edge of Mohave Desert); flowers with calyx but no corolla.
4. Leaves typically simple, sometimes 3; solitary or terminal leaflets broad ovate to rounded, subcuneate, usually obtuse or retuse at tip, margin entire to crenate. Monoecious; usually shrubby. Bark dark brown or reddish, thickish, narrowly ridged, with small scales
F. anomala Torr. var. *anomala* (single-leaf ash)
4. Leaves compound, mostly 5-foliolate; terminal leaflet usually obovate, cuneate at base, margin crenate-serrate. Dioecious; small Arizona tree
F. anomala var. *lowellii* (Sarg.) Little (Lowell ash)

1. Twigs terete.
2. Eastern species; corolla absent.
3. Lateral leaflets sessile, 3–5 pairs, nearly glabrous except at first, long-acuminate; calyx none; mostly polygamous. *Additional characters*: Twigs stout, yellowish, with large pale lenticels; buds black, acute, the upper scales pinnate; leaf-

scars large, round; leaves dull dark green, 12–16 inches (3–4 dm) long; samara-body flattened, winged all round. Northern, often slender tree of stream-banks and swamps, bark grayish brown, somewhat corky. Wood rather heavy, medium soft and weak, brown

F. nigra Marsh. (black ash)

3. Lateral leaflets stalked; calyx present—at least in fertile flowers; dioecious.
4. Leaflets mostly entire or nearly so, usually 7, pale beneath and more or less velvety-pubescent, hairy or woolly, with impressed yellow midribs. Tall swamp tree with light gray bark and enlarged buttressed base. *Additional characters*: Twigs velvety-hoary first season; buds ovoid, obtuse, pale-pubescent; leaf-scars deeply concave at top; leaves 9–18 inches (23–46 cm) long; leaflets of an oblong-lanceolate type, acuminate, 5 inches (12.5 cm) long or more, petiolules unwinged; small campanulate 4-lobed calyx; stigma bifid; samara 2–3 inches (5–7.5 cm) long, the body slightly compressed and not sharply contrasted with ½ inch (12 mm) wide wing. Wood light, soft and brittle

F. profunda Bush (pumpkin ash)

4. Leaflets mostly toothed; twigs, when they appear, more or less pubescent, hairy, or woolly but usually glabrescent.
5. Buds mostly acute, small, brown-puberulent, the lowest or outermost scales rounded and short; leaflets long—(about 10 mm) petioluled; samaras broadly spatulate, nearly 2 inches long. *Additional characters*: Leaves 5–12 inches (12.5–30 cm) long; leaflets mostly 5–7, usually acuminate; samara-body flattened, winged all round, the wing broad. Small southeastern swamp or river-bank tree with light gray, rather thin bark with small thin scales; often an understory or associate of baldcypress. Wood light, soft and weak, brownish or yellowish white

F. caroliniana Mill. (Carolina ash)

5. Buds mostly obtuse, the lowest or outermost scales acute; leaflets shorter-petioluled; samaras narrowly spatulate, narrow-winged, the body terete or nearly so. Wood heavy, hard, strong, brownish.
6. Leaf-scars more or less horseshoe-shaped, half-round in outline but deeply concave at apex; twigs stout, "stubby" and brittle, with pale lenticels; leaflets pale or whitish beneath; samara-wing only slightly decurrent. *Additional characters*: Buds rusty to dark brown or blackish, broad, inner scales shiny; leaves 8–12 inches (2–3 dm) long; leaflets 5–9, smooth and glabrous or somewhat puberulent beneath, lanceolate or elliptic-lanceolate to nearly oval, acute or acuminate, nearly entire to somewhat inconspicuously toothed, dark green and lustrous above. Large tree with ridged, dark brown to reddish gray bark; the most important economically of our native ashes

F. americana L. (American ash)

6. Leaf-scars half-round but either truncate or only slightly concave at apex; twigs more slender and elongated than in *F. americana*, velvety-pubescent or downy, especially toward the tips (but glabrous in *F. pennsylvanica* var. *subintegerrima* (Vahl) Fern., syn. *F. lanceolata* Borkh.); leaflets green on both sides; samara-wing decurrent almost but not quite to the body base. *Additional characters*: Buds rusty-woolly, the inner scales sometimes pinnately cut at tip; leaves 10–12 inches (2.5–3 dm) long; leaflets 7–9, mostly 7, up to 6 inches (1.5 dm) long, thin, serrate, from narrowly elliptic or lanceolate to oval; samaras 1–2½ inches (2.5–6 cm) long, mostly under 2 inches (5 cm) long, the body slender, sharply contrasted with wings and tapering to a sharp point at base. Medium-sized to large tree of rich bottom-lands and slopes; bark shallowly furrowed, reddish brown, the inner bark reddish

F. pennsylvanica Marsh. (green ash)

2. Western species.
3. Pacific tree of timber size. Twigs stout, pale, often beset with whitish or brownish hairs; leaflets 5–7, entire or toothed above middle, 2½–7 inches (6.5–17.5 cm) long, the laterals often sessile; bark thick, dull dark gray to grayish or reddish brown, deeply and narrowly furrowed with broad flat ridges. Wood hard, medium light, rather brittle, brownish. (The tree from which Fresno and Fresno County, Calif., derive their names.)

F. latifolia Benth. (Oregon ash)

3. Southwestern, mostly small trees or shrubby; lateral leaflets relatively small.
4. Rachis narrowly winged; leaflets small, ½–3 inches (1.2–7.5 cm) long; twigs slender.
5. Leaflets commonly 3–5 (varying 1[1]–7), ½–2, rarely 3 inches (1.2–7 cm) long,

[1] In the var. *nummularis* (Jones) Little.

subcoriaceous, of a spatulate type, entire or crenulate, the margin reflexed, sessile, obtuse or acutish, small-black-dotted below, the old leaves persistent until flowers appear. *Additional characters*: Twigs slender, glabrate, when young slightly gray - puberulent; samara - wing slightly decurrent at apex, the body thick; bark smooth, thin, iron-gray with large papery scales. (w. Tex.-n. Mex.). . *F. greggii* A. Gray (Gregg ash)

5. Leaflets commonly 7 (varying 5–9), thinner, sessile, crenulate or serrulate above the middle, the margin flat or only slightly reflexed; leaves 1–3¼ inches (2.5–8 cm) long; twigs (as also buds and petioles) densely tomentose with stellate fulvous hairs, slender; samara-wing decurrent nearly to body base. (s. Ariz.-n.e. Sonora)

F. gooddingii Little (Goodding ash)

4. Rachis not winged (except rarely in *F. cuspidata*); leaflets averaging somewhat larger, 1–4 inches (2.5–10 cm) long.

5. Terminal buds acute, about ½ inch (12 mm) long; leaf-scars elevated, crescent-shaped.

6. Twigs slender; leaflets not bluish beneath; flowers conspicuous.

7. Leaflets usually 7, lanceolate or oblong-lanceolate, 1½–3 inches long, coarsely serrate. *Additional characters*: Leaf-scars dark; terminal bud mahogany-colored, resinous; leaflets beset with minute black dots beneath; samaras elliptic to oblong-obovate, ⅓–1 inches (8–25 mm) long. Corolla present, 4-lobed, fragrant. (w. Tex-n.w. N. Mex.-n. Mex.). *F. cuspidata* Torr. var. *cuspidata* (fragrant ash)

7. Leaflets usually 3–5 (occasionally simple), often ovate, about 1–1½ inches (25–37 mm) long, usually entire; body of fruit thin. (n. and centr. Ariz.-s.e. Nev.).

F. cuspidata var. *macropetala* (Eastw.) Rehd. (longpetal ash)

6. Twigs stout; leaflets bluish white and papillose beneath; flowers inconspicuous.

7. Leaflets sessile, 5–9, elliptic to oblong or ovate, 1–2½ inches (3–6 cm) long. (s.w. N. Mex.-s.e. Ariz.-n. Mex.)

F. papillosa Lingelsh. (Chihuahua ash)

7. Leaflets stalked, mostly 5, ovate-obovate, rounded or acute at tip, thick and firm, 1–3 inches (2.5–7.5 cm) long; calyx persistent. (Tex.-Okla.)

F. texensis (A. Gray) Sarg. (Texas ash)

5. Terminal buds small, about ⅛ inch (3 mm) long; leaf-scars not crescent-shaped; twigs slender.

6. First-year twigs pubescent or woolly (var. *glabra* Lingelsh. has glabrous or nearly so twigs and leaves); samaras not over ½ inch (12 mm) long; leaf-scars large, obcordate, dark. *Additional characters*: Leaflets 3–5, 1–3 inches (2.5–3.5 cm) long, thickish, greenish and mostly pubescent or tomentose beneath. The vars. *glabra* and *toumeyi* (Britt.) Rehd. have distinctly stalked (instead of sessile) leaflets. (w. Tex.-s.w. Utah-s. Nev.-s Calif.).

F. velutina Torr. (velvet ash)

6. First-year twigs glabrous; leaf-scars small, elevated, round; samaras to 1½ inches (37 mm) long. Leaflets of an elliptic type, mostly acuminate, 3–4 inches (7.5–10 cm) long. (s. N. Mex.-s. Ariz.-n. Mex.).

F. berlandieriana A. DC. (Berlandier ash)

LAMARCK'S FIVE AMERICAN ASH TYPES

Under the heading "FRÊNE, *FRAXINUS*" Lamarck (Encylopèdie Méthodique Botanique **2:** 544–549. 1786) and the subhead "Frênes du nouveau Continent; les feuilles n'ont la plupart que sept ou neuf folioles" (p. 547–549) described five new American ashes, numbered 5 to 9, inclusive. The late Professor Fernald, in his paper *Noteworthy plants of southeastern Virginia* (Rhodora **40:** 434–459, illus. Nov. 1938) stated:

> That *F(raxinus) profunda* Bush (1901), at least as to its eastern phase, is *F. tomentosa* Michx. f. (1813) is unquestionable. Whether it is also *F. pubescens* Lam. (1786) I can more easily tell when a photograph of Lamarck's type reaches me from Paris . . . . By an easy wave of the hand demoting, without examining the types, most of the species proposed by Lamarck, Bosc, Michaux filius and others of 100 to 150 years ago, to the unquestioned synonymy of a few species of Linnaeus, Miller and Marshall, the way was cleared for new propositions. Until the types of all the early-proposed species have been most intelligently checked the names of our American ashes will remain hopelessly tentative.

On writing Dr. Rollins at the Gray Herbarium I was informed that he could

FIG. 1.—*Fraxinus acuminata* Lam.: Type.

find no evidence of the existence of any photographs of Lamarck's *Fraxinus* types at that institution. I thereupon wrote Prof. H. Humbert, curator of the Laboratoire de Phanérogamie, Muséum National d' Histoire Naturelle in Paris, and, through his kind assistance, have obtained photographs of these types (Figs. 1–5). All are sterile except the specimen of *F. pubescens* Lam. Brief comment on these five photographs follows:

1. FIG. 1, Lamarck's no. 5, "Frene acuminé, *Fraxinus acuminata* . . . N." Lamarck questions if this may not be the same as *F. americana* L. There seems to be no question but that this leaf is actually of *F. americana* L. Somebody (perhaps Lamarck himself) has written "fraxinus americana L." on the mounting sheet. Lamarck gives the common names as "Frêne de la nouvelle Angleterre, Frêne blanc d'Amerique" and says that the leaflets are "subtus glaucis"—all of which besides the general appearance, agrees with *F. americana*. Moreover, Sargent (The Silva of North America **6:** 43. 1894), Sudworth (Nomenclature of the Arborescent Flora of the United States, U. S. Dept. Agr., Div. For. Bull. 14: 326. 1897), and Rehder (Bibliography of Cultivated Trees and Shrubs Hardy in the Cooler Temperate Regions of the Northern Hemisphere, p. 557. 1949) all agree that *F. acuminata* Lam. is a synonym of *F. americana*.

2. FIG. 2, Lamarck's no. 6, "Frene à feuilles de Noyer, *Fraxinus juglandifolia* . . . N." Sargent (*op. cit.*, p. 43 and 55) tentatively refers *F. juglandifolia* Lam. both to *F. americana* and *F. caroliniana*. Sudworth (*op. cit.*, p. 330) refers the species with a question mark to *F. caroliniana* Mill. Rehder (*op. cit.*, p. 557) makes the species a synonym of *F. americana* var. *juglandifolia* (Lam.) D. J. Browne. Little [Check List of Native and Naturalized Trees of the United States (including Alaska). U. S. Dept. Agr. Handbook 41: 188. 1953] remands both names to synonymy under *F. americana*, though (p. 11) he states that his nomenclature places "emphasis on names useful to foresters and other field workers, rather than on names based upon minute differences distinguished only by specialists in plant taxonomy." Some of Lamarck's phrases, such as "folioles . . . blanchâtres en

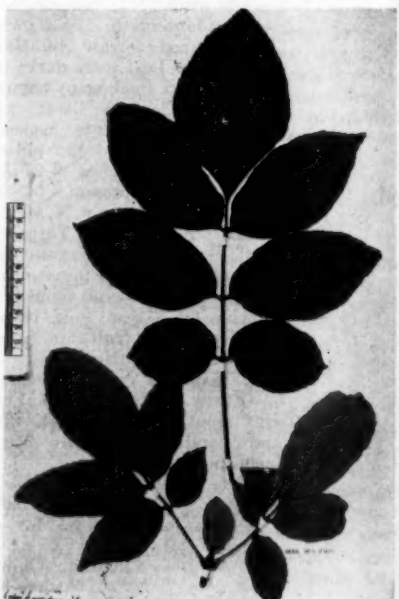


FIG. 2.—*Fraxinus juglandifolia* Lam.: Type.

dessous," the fact that the leaflets in the type are crenulate-serrate (the teeth hardly acute) and relatively short-petioluled tend, in my opinion, to agree with Rehder and Little that *F. juglandifolia* Lam. is a form of *F. americana* L. and, if one prefers, is var. *juglandifolia* (Lam.) D. J. Browne.

3. FIG. 3. Lamarck's no. 7, "Frene de Caroline, *Fraxinus Caroliniana*" new var. "*β*" known locally as "Frene de la perspective." This variety is said to have longer, narrower and more acute leaves than the typical form. Lamarck further states "Ces fleurs de développent en Mai, en même temps que les feuilles," which seems more apropos of green ash than of Carolina ash. As "*β*" has no present nomenclatural significance and the type is fragmentary it seems unnecessary to comment further except to suggest that both description and photograph strongly point to *F. pennsylvanica* Marsh. var. *subintegerrima* (Vahl) Fern., syn. *F. p.* var. *lanceolata* (Borkh.) Sarg.

4. FIG. 4, Lamarck's no. 8, "Frene pubescent, *Fraxinus pubescens* . . . N." This is the only one of Lamarck's American ash types that shows an inflorescence. Sargent (*op. cit.*, p. 49), Sudworth

FIG. 3.—*Fraxinus caroliniana* Mill. var. *β* Lam.: Type.

FIG. 4.—*Fraxinus pubescens* Lam.: Type.

(*op. cit.*, p. 328), and Rehder (*op. cit.*, p. 558) all agree that *F. pubescens* Lam. is a synonym of *F. pennsylvanica* Marsh. This unanimous opinion of distinguished authority would appear to settle the matter but I believe the decision is still open to question. It is generally accepted that *Fraxinus tomentosa* Michx. f. (1813) and *F. profunda* Bush (1897) are synonymous. The former name is adopted for pumpkin ash in ed. 8 of Gray's Manual and in Gleason's "New Britton & Brown Illustrated Flora" (1952) but Little (*op. cit.*, p. 193) has shown that the name *F. tomentosa* Michx. f. is illegitimate under Code Art. 73(1). It is of interest that the younger Michaux's "*foliolis subnovenis, dentatis, petiolatis, ramulis petiolisque pubescenti-tomentosis*" is a repetition of Lamarck's description of his *F. pubescens* except that Lamarck adds "floribus calyciferis" and "*Fraxinus ornus americana.* Hort. Reg." Lamarck's description of the pubescence might apply to either green or pumpkin ash but perhaps even better to the latter: "Ses petits rameaux & les pétioles de ses feuilles sont constamment couverts d'un duvet cotonneux, fort court, cendré & doux au toucher . . ." The pistillate

calyx is described as small, monophyllous, campanulate, glabrous, parted into 4 straight divisions, containing a style "long d'environ cinq lignes" (10 mm). *Fraxinus profunda* is noteworthy for its *relatively* large (about 3 mm long) pistillate calyx. In the photograph furnished by the Paris Museum (Fig. 4) the calyces are not sharply delineated and magnification accentuates the defect; however, they appear to be about 2.5 mm long; that feature, coupled with Lamarck's statement "l'ecore est grisâtre", lends some plausibility to a guess that this specimen might be pumpkin ash. It is hoped that some botanist in or visiting Paris will study this specimen carefully, measure the calyces and also examine the tree (provided it be still standing) to which Lamarck refers. If it is in fact pumpkin ash, the name *F. pubescens* Lam. obviously will have priority over *F. profunda* Bush.

FIG. 5.—*Fraxinus sambucifolia* Lam.: Type.

5. FIG. 5, Lamarck's no. 9, "Frene à feuilles de Sureau, *Fraxinus sambucifolia* . . . N." The photograph resembles a somewhat juvenile spray of black ash (*F. nigra* Marsh.); the description also suggests black ash. Sargent (*op. cit.*, p. 37), Sudworth (*op. cit.*, p. 325), Rehder (*op. cit.*, p. 560), and Little (*op. cit.*, p. 192) all remand *F. sambucifolia* to synonymy under *F. nigra*. That appears to be the correct disposition of the name.

ENTOMOLOGY.—*The flight mechanics and evolution of the wings of Ephemeroptera, with notes on the archetype insect wing.*[1] GEORGE F. EDMUNDS, JR., University of Utah, and JAY R. TRAVER, University of Massachusetts. (Communicated by Herbert H. Ross.)

The classification of the Ephemeroptera, or of any other group of organisms, should be based upon the phylogeny of the group or, to be more precise, upon a reconstruction of the probable phylogenetic relationship as indicated by all available evidence. This paper presents the results of one phase of an investigation into the problem of establishing a more natural classification of the order Ephemeroptera. The wings of mayflies have been used as a primary evidence of relationship among extant mayflies and have been the principal evidence available for the classification of fossil forms, many of which are known only as wing prints. To utilize this data to the full it is necessary to be exact in determining the homology of veins and other structures. Thus it was considered necessary to re-examine critically the problem of the wing venation and structure of the mayflies and their fossil allies.

As the study progressed it was realized that there was a correlation between wing structures and the flight pattern of the mayflies studied. This led to an extensive study of the mechanics of flight of the Ephemeroptera. As the Ephemeroptera are

[1] This paper is modified from a thesis submitted to the University of Massachusetts in partial fulfillment for the requirements of the degree doctor of philosophy. Dr. Jay R. Traver collaborated extensively on this section of the thesis. The research was supported by financial assistance from the University of Utah Research Fund.

apparently the most primitive of all winged insects, it was subsequently necessary to enter into some of the basic problems concerning the origin and evolution of the insect wing.

STRUCTURE AND MECHANICS OF THE MAYFLY WING

The wing[2] of a mayfly (Fig. 1) is somewhat triangular in outline and has a regular series of corrugations or fluting, which gives it a fanlike form. Each longitudinal vein follows along the crest of a ridge or the bottom of a furrow. Veins that follow ridges are called convex (indicated by a + sign in the figures); those that follow the bottom of the furrows are called concave (− sign). At the margin of the wing there is a complete alternation of concave and convex veins. These corrugations, much as in a fluted fan, greatly strengthen the wing and make it quite rigid. The convex veins and their attached crossveins and membranes act as braces to keep the wing rigid on the downstroke, and the concave veins and their attached crossveins and membranes act as braces to maintain rigidity on the upstroke.[3] The anterior margin of the wing is further strengthened by the close grouping of the costa, subcosta, and radius 1, which are held together at the base by the costal brace. This brace is attached to the convex costa and radius, while the concave subcosta lies between and below and is held firmly in place by the floor of a cup-shaped depression (Fig. 2).

As a result of the above-mentioned structure, the mayfly wing would seem to be rather rigid. This is not entirely so, however, for some of the main longitudinal concave veins, namely Sc, R_{2+3}, MP_1, and sometimes MP_2, have weakened spots called bullae (Fig. 3). In *Siphlonurus* and most of the mayflies, the last vein with a bulla is MP_1, but in some specimens of *Cinygmula* bullae were observed on MP_2. The bullae allow the concave veins to bend, and consequently, during the upstroke, the concave veins fail to support the distal half of the wing. From these facts it can be seen that the corrugations or fluting of the wing and the bending allowed by the bullae serve important flight functions. On the downstroke the wing remains rigid, and the insect gets a maximum amount of lift and propulsion from the stroke (Fig. 4). On the upstroke, however, the distal half of the wing bends downward under the pressure of the opposing air because of the failure of the concave veins, which are weakened by the bullae, to support the wing tip (Fig. 5). The opposing air thus slips away in such a manner as to offer lessened resistance to the upstroke of the wing. The wing tip is the most effective portion of the wing surface because the arc through which the wing travels and the moment of force both become greater as the distance of the wing surface from the point of attachment to the thorax increases.

When the upper and lower surfaces of the wing are separated by soaking in caustic potash it is seen that the costal vein and costal crossveins are equally represented on both surfaces of the wing. All other convex veins are developed almost entirely on the upper surface of the wing, and the concave veins are on the lower surface. Crossveins are found on the upper surface except at the end that attaches to the concave veins where a distinct short section is found on the lower surface (Fig. 6). The veins and crossveins are arranged on the wing surfaces in such a way as to give maximum support during flight. The greatest stress falls on the convex veins and they are noticeably larger than the concave ones. The crossveins are arranged so as to give support on both upstroke and downstroke but the major development of these veins is in that part that attaches to the convex veins.

In the higher winged insects the anterior margin of the wing is quite rigid, and the remainder of the wing membrane is comparatively flexible. These insects fly by means of a sculling action of the wing in which the rigid anterior margin leads the membrane in the direction of the wing stroke. As the wing moves downward, the membrane is inclined upward. This drives the air backward, giving forward thrust, as well as causing a reduced pressure area anteriorly into which the insect is drawn.

In the Ephemeroptera the folding along the line of the bullae (Figs. 1, 5) inhibits sculling

[2] Reference is always to the forewing, unless otherwise specified.

[3] The physical principles involved in strengthening a plane surface by fluting are widely used in engineering. The fact that corrugated steel is much more rigid than flat sheets depends on the same physical principles as does that of the wing of a mayfly. The fact that the support is primarily a one-way support is readily demonstrated by a common steel rule as used by carpenters, *et al.* When held with the concave surface up, such a rule is so rigid that it supports itself when extended to full 6-foot length, but is so flexible as to roll readily into a small circular case when bent in the opposite direction.

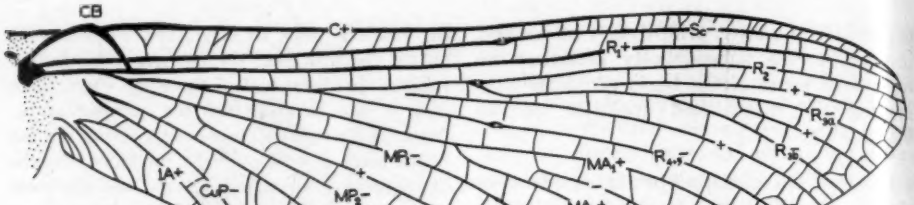


FIG. 1.—Forewing of *Siphlonurus*, showing the bullae and convex (+) and concave (−) veins. FIG. 2.—Enlargement of wing base in costal region showing the costal brace (CB) and the pleural wing recess (PWR). FIG. 3.—Enlargement of bulla at fork of R_2 and R_3.

action to a noticeable degree. It is probable, therefore, that the mayflies obtain their forward thrust primarily from the downstroke, but even then sculling action is not especially effective.

With no problems of obtaining food, the adults of Ephemeroptera have almost every structure adapted for reproductive activity. The wings appear to be no exception to this. The nuptial flight of most mayflies consists of flying upward and then passively coasting or leisurely flying downward. In most species the lines of flight are mainly vertical. The mechanics of flight thus seems to be well adapted for this particular behavior pattern. The corrugation or fluting of the wings also appears to give stability to the downward sailing motion with the wings motionless. Even though the Ephemeroptera have a very primitive wing type, the wing structure is specialized to the degree that it is closely correlated with the behavior of the nuptial flight.

An intensive study was conducted on the wings of *Siphlonurus*, but the other members of the Siphlonuridae, and representatives of the Ametropodidae, Heptageniidae, Baetidae, Leptophlebiidae, Ephemerellidae, Baetiscidae, Ephemeridae, and others, show a similar structure and presumably have similar flight mechanics. The theories of flight functions gained by a study of the wings were tested extensively by means of paper models which performed in the manner which had been already hypothesized on the basis of the study of the structure of the wings. Many direct observations upon the wing motion of the larger mayflies such as *Hexagenia* and *Ephoron* also corroborated these findings to some extent.

An examination of the wings of mayflies belonging to a number of genera indicated some correlation between the degree of development of the bullae and the wing shape. In the genera with long and narrow wings, the bullae are usually well developed on the anterior four, and sometimes five, longitudinal concave veins. Genera possessing shorter and broader wings usually have fewer bullae, feebly developed (probably vestigial) bullae, or both.

THE ARCHETYPE WING

The oldest winged insects are found in the

upper Carboniferous, but it is evident from the great variety of wing types in these fossils that the first winged insects are of greater antiquity. Thus, on the basis of evidence available from the study of fossils and development, entomologists have been forced to speculate on the nature of the first insect wings.

Throughout the winged insects one finds evidence of concave and convex veins. The presence of such a condition led Adolph (1879), and later Lameere (1922), to propose nomenclatorial systems based on the concave or convex positions of the veins.

Forbes (1943) discusses in detail the probable stages in the development of the first wings in insects. He points out the probability that the original wing was a thick process, and he believes that the areas between the veins thinned out and the veins became the main strength of the wings. The present study of the mechanics of the wings of Ephemeroptera has led the writers to believe that the thinning of the wings and the origin of fluting in the wings were simultaneous. As the wings thinned out they needed support, and it is doubtful if the veins themselves could have provided the necessary rigidity. The combination of veins and fluting certainly could have provided better support than the veins alone. That the fluted surface would have provided greater rigidity than a flat surface is easily demonstrated by comparing the rigidity of a flat piece of paper to one that has been fluted by folding. The importance of the veins in establishing this rigidity is pointed out by the fact, as has been mentioned above, that the wing tip loses its support because of the desclerotized areas or bullae on a few principal longitudinal veins.

The actual origin of fluting of the wings is lost in antiquity, but some ideas concerning it have been offered. Needham (1935a) would attribute its origin to the gathering together of the basal connections of the veins as the base of the wing narrowed. Forbes (1943: 393) explains it by the articulation and muscle attachment of a few principal veins to the thorax.

However, once fluting actually started, from whatever cause, it would increase the rigidity of the wing. Once a wing membrane was made more rigid by the fluting, it would have been possible for the wing membrane to become thinner without deleterious effect on the flight powers of the insect.

On the basis of a study of the wings of all groups of insects, living and fossil, Comstock and Needham (1898), arrived at a concept of the hypothetical archetype wing venation (see Comstock 1918: 19). After Lameere (1922) pointed out that the media was composed of two elements, an anterior convex and a posterior concave portion, Bradley (1931) presented a modified hypothetical archetype which included MA. This archetype was modified by Snodgrass (1935: 216) to include the two branches to the anterior division of the cubitus, which had been pointed out earlier by Tillyard (1919). The drawing from Snodgrass has been copied herein (Fig. 7),[4] but the branches of the cubitus have been relabeled to conform to the venational terminology of this paper and signs have been added to indicate the concave or convex positions of the veins.

We herewith propose the hypothesis that the first winged insects possessed a wing that was completely fluted, i.e., had a complete alternation of concave and convex veins at the margin of the wing. Therefore, a modified archetype venation is herein offered (Fig. 8) which includes the intercalary veins necessary for a completely fluted wing. Of necessity, such an archetype venation must include the so-called intercalary veins that are typical of many fossil forms and of some modern orders, principally the Ephemeroptera. Comstock (1918) refers to intercalary veins as veins which arose without a basal attachment, and cites the ephemerid wing as an example. The fossil record clearly demonstrates, however, that the intercalaries of the mayflies were originally attached veins, and that detachment at the base has been a subsequent specialization. A number of the features of the archetype venation are highly questionable because of their great variability in primitive groups. There is reason to believe that subcosta was originally an unbranched vein and that the so-called Sc_1 is merely a realigned crossvein while Sc_2 is the true Sc. It is uncertain as to whether MP should still be considered to be four-branched or if it should be only a 2-branched vein. In what we consider to be the most primitive type of wing as seen in the Syntonopteridae it is only 2-branched, but even the Syntonopteridae have wings that have undergone considerable evolution. Those Palaeodictyoptera that have more than two branches to MP appear to have more specialized wings than do the Syntonopteri-

[4] From *Principles of insect morphology*, by R. E. Snodgrass, courtesy McGraw-Hill Book Co., Inc.

dae. It is, of course, possible that such a wing as illustrated in Fig. 8 could have been the precursor of the Syntonopteridae and those Palaeodictyoptera with more than two branches to MP. The evidence is not sufficient in our estimation to necessitate a relabeling of the branches of MP in the ephemeropteran wing to indicate the possible 4-branched condition in the ancestral stock.

In the foregoing discussion it has been pointed out that fluting actually is a severe detriment to the sculling action of flight. There seems to be little doubt that the sculling type of flight is superior to that of the mayfly type. It is our belief *that fluting of the wing surface was important to the first winged insects for the purpose of strengthening the wing surface and was a necessary requisite before the wing could thin out and form an effective surface for flight. Yet once the wing became thin, fluting actually is detrimental to sculling flight except in the few veins near the anterior margin where rigidity is still required. The trend in the evolution of insects is, in most cases, toward wings which have a rigid anterior margin with a flexible membrane behind.* This type of wing is well adapted for speed in flight, while the fluted wings are essentially lift-type wings. None of the remarks above are intended in the Lamarckian sense, but are meant only to imply that the mechanical fitness of any variation in the wing is the principal selective force determining the general direction of the evolutionary trend. Simpson (1950) has recently remarked that most major trends in evolution are adaptive, and it would appear that this is certainly true in the case of wing structure and venation of insects.

It may well be that the mayflies have maintained functional fluting only because of their unique vertical flight habits, which are dependent upon the bullae.

A number of changes in the venation of the wings of insects seems to bring about flexibility in the wing by destroying functional fluting. A few of these noted during the present study are: (1) the shifting of the position of the longitudinal veins so as to cause them to diverge to the rearward; (2) broadening and shortening of the wing (this often aids process 1, above); (3) migration of concave veins to the vicinity of, and subsequent fusion with, convex veins; (4) elimination or atrophy of intercalary veins; (5) staggering of the path of a vein; (6) desclerotization of veins; and (7) atrophy of crossveins.

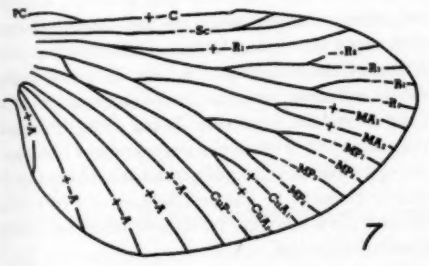
The weakening of the wing membrane beyond a certain point is detrimental and those insects which are strong fliers continue to have a well developed system of veins. The problem is most easily explained by the analogous case of fanning air into a fire. If one selects a flat board and waves it much in the fashion of the action of an insect wing, he will find that it is quite ineffective. A small piece of rug which can be held stiff on one margin, however, has a fine sculling action and is much more effective. If for a final test one selects a piece of cloth or paper and holds one edge stiff, the material will prove so pliable as to be of little value in moving air. The wing operates in much the same manner. A wing membrane that is either too rigid or excessively pliant is ineffective; the most effective degree of pliancy is intermediate between the two extremes and undoubtedly varies according to the size and shape of the wing, loading, speed of flight, wing beat frequency, atmospheric pressure, and numerous other factors.

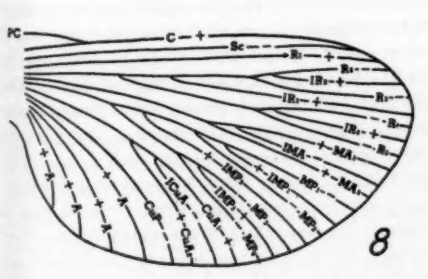
Another evolutionary trend that has been significant in providing an effective sculling surface for insect flight has been the inclusion of the hind wing surface with the forewing by means of coupling devices. Such wing coupling is well known in such insect orders as Lepidoptera and Hymenoptera, but it also occurs in the Ephemeroptera. We have noted such coupling devices in certain Palingeniidae, Polymitarcidae (Campsurinae), Oligoneuriidae, and Siphlonuridae, and a survey of the order may prove wing coupling to be more common than suspected.[5] The nuptial flight pattern of certain Heptageniidae suggests that there is a greater sculling action than the forewing alone would be expected to provide and that the two pairs of wings may be coupled.

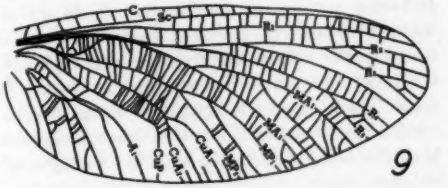
Among the smallest insects where the surface area of the insect is large in relation to volume one finds a wide variety of wing types. Many have greatly reduced venation as in the Coccidae, various parasitic Hymenoptera and the tiny Diptera, but even when the wing venation is reduced to an apparent single vein, this is along or near the costal margin of the wing. With reduction of the size of an insect there is an accompanied reduction in the number of wing

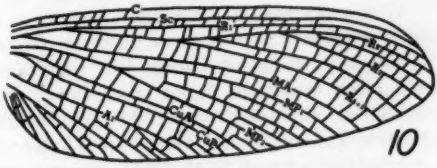
[5] Dr. Georges Demoulin has informed us (*in litt.*) that all Palingeniidae, Polymitarcidae (including Campsurinae), Euthyplociidae, and Isonychiidae, which he has examined have the hind wings coupled to the forewings.

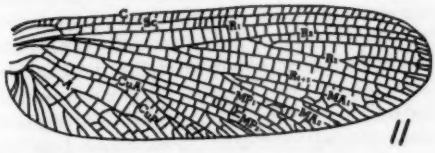
veins. Dr. H. H. Ross has informed one of us (personal conversation with G. F. E., Jr. December 1953) that the order in which the wing veins drop out shows a regular parallel development in five separate phyletic lines of caddisflies in which reduction of the size of the insect has taken place. Because of the reduced venation among smaller forms, small species are rarely of value in attempting to arrive at a generalized wing venation pattern of any particular taxon.

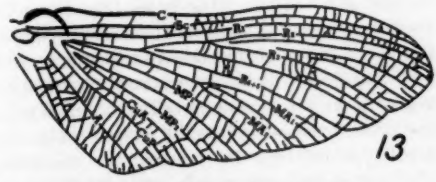












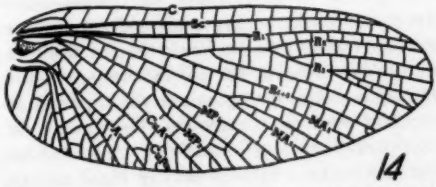


FIG. 4.—Forewing of *Siphlonurus* at midpoint of the downstroke. FIG. 5.—Forewing of *Siphlonurus* at midpoint of upstroke. FIG. 6—Cross section of anterior area of forewing of *Siphlonurus*, with ventral and dorsal surface separated. FIG. 7.—Hypothetical archetype venation (modified from Snodgrass, 1935). FIG. 8.—Hypothetical archetype venation as proposed herein. FIG. 9.—Hind wing of *Lithoneura mirifica* Carpenter (modified from Carpenter, 1944). FIG. 10.—Diagram of hind wing of *Triplosoba pulchella* (Brongniart) (modified from Tillyard, 1932). FIG. 11.—Hind wing of *Protereisma permianum* Sellards (modified from Tillyard, 1932). FIG. 12.—Forewing of *Protereisma gracile* Sellards (modified from Tillyard, 1932). FIG. 13.—Forewing of *Baetisca rogersi* Berner (modified from Berner, 1940). FIG. 14.—Forewing of *Misthodotes obtusus* (Sellards) (modified from Tillyard, 1932).

Among the smallest insects occur also the forms with fringed wings as in the Thysanoptera, Hymenoptera (i.e., Mymaridae), Coleoptera (Orthoperidae or Corylophidae, and Ptiliidae or Trichopterygidae), Diptera (Nymphomyidae), and some of the small Lepidoptera. Even among these fringed-wing insects the density of the fringe on the wing is directly correlated with size, the larger species having the denser fringe of setae. The independent aquisition of the fringed-wing type by several orders of insects suggests that this wing is particularly suited for flight by smaller insects.

Within the Ephemeroptera representatives of several families seem well on the way toward abandoning functional fluting, and some have completely abandoned fluting and present a well developed sculling-type wing. Members of the families Caenidae and Tricorythidae show a parallel development in that the wings of both are extremely broad and short, the cross venation is greatly reduced, bullae are not evident, and fluting is poorly developed. All of the Caenidae have lost the hind wing and it is much reduced or wanting in the Tricorythidae. The flight of both *Tricorythodes* and *Caenis* differs from the usual type in being rapid with a short vertical undulation.

In the Palingeniidae and Behingiidae the essential fluting has been altered in the radiomedial area by the migration of the concave veins to the vicinity of the convex veins. In the Oligoneuriidae there is a series of genera which show various degrees of fusion of the concave with the convex veins. In *Pseudoligoneuria*, whose wing venation is known only from a study of the nymphal wing pads, the venation apparently approximates the usual type although the concave veins are weak. The genera *Oligoneuriopsis* and *Oligoneuriella* have very weak concave veins which lie next to the convex veins. In *Lachlania* the concave veins lie in folds beneath the convex veins, while in *Homoeoneuria* and *Oligoneuria* the fusion is apparently even more complete. This family (except perhaps *Pseudoligoneuria*) no longer exhibits the conventional type of mayfly flight and has developed a sculling type of flight. The veins have no bullae, crossveins are greatly reduced, and the veins behind R_1 are divergent from the longitudinal axis of the wing. Also the wing membrane remains pliant because these mayflies fail to shed the subimaginal pellicle from the wings—it is shed only from the body, legs, and tails. The flight of *Lachlania* lacks the typical vertical pattern, and is extremely rapid and powerful. We have observed males of *Lachlania* making progress upwind against a breeze that would drive individuals of most other mayfly genera from the air. Mayflies of this genus have an excellent flying power that clearly demonstrates the superiority of the sculling type of flight for speed and power.

If functional fluting is maintained, as it is in most mayflies, the venational changes, except for modifications in the basal connections or path of a vein, are distinctly limited. Almost all changes in the main venational pattern fall into the categories of either (1) branching of existing veins with the formation of an intercalary vein, or (2) simple fusion of two branches of the same vein with the elimination of the intervening intercalary.

As functional fluting disappears changes in the venation are not as limited, and may include such possibilities as: (1) atrophy of a vein; (2) addition of a vein; and (3) fusion of veins of opposite sign, i.e., a concave and a convex vein. Even when one considers the great number of venational changes that are possible, it seems that many have come about primarily by simple fusion of the branches of a vein. It would cause much less upset in the mechanical action of a wing to reduce a vein by fusion of its branches than it would if the vein were to drop out completely. Students of wing venation should give serious thought to the possibilities of explaining present wing venation by fusion before assuming that a vein is lost.

Except for the veins along the anterior margin of the wing, fluting or alternation of concave and convex veins would seem to be of little use to insects that have a sculling type of flight. Also there is no apparent reason why convex veins should belong to the upper surface and concave veins to the lower surface in such forms. Yet, the fluting of wing veins is found in practically every order of insect and even when fluting is obscure, the separation of the wing surfaces often reveals which veins are concave and which are convex. The logical explanation appears to us to be that the fluted type of wing is the ancestral type and that the convex and concave vein positions are nonfunctional in most modern insects and are to be regarded as vestigial conditions. If this is true, then the concave or convex positions of veins should be valid evidence for establishing vein homologies. The present study, however, points out one possible pitfall

in using this evidence alone. In the wing of *Lachlania* where the concave veins are now in the process of fusing with the convex ones, R_3 has lost its identity by having its distal half under IR_3. Thus, in a fundamentally concave area of the wing, it is evident that the sole surviving vein in the center of the radial sector will be a convex intercalary.

In many groups of insects a careful study of concave and convex vein positions will, when used in conjunction with other evidences, lead to a more clear exposition of wing vein homologies. Positional evidences are the most important single evidence in interpreting vein homologies in the Ephemeroptera; without this evidence determination of the venational homologies of the highly modified wings of the Oligoneuriidae would probably have been impossible. In other groups of insects in which the wings are greatly modified venational positions will probably yield a minimum of evidence. In some insects some of the wing veins are convex at the base and concave distally (or vice versa). In such cases the vein positions may be a result of secondary modifications but in others such evidence may aid in interpreting vein fusions. An example of the latter type is found in the dragonflies, where the concave subcosta has fused with the convex costa beyond the nodus and has imparted a concave nature to the combined costa and subcosta along the leading edge of the wing.

ORIGIN AND EVOLUTION OF THE EPHEMEROPTERA

If the archetype venation proposed herein is accepted, the most primitive known winged types are found in the family Syntonopteridae of the Palaeodictyoptera. The main difference between syntonopterid venation and that of the archetype is that R_3 has formed a triad (although this may have been an archetype feature), and there have been some changes in the basal connections in the hind wing. In the genus *Syntonoptera*, MA is independent of Rs, but in *Lithoneura* (Fig. 9) MA has branched anteriorly near the base to fuse for a short distance with Rs. Carpenter (1938: 450) remarks that "It is very probable that the family Syntonopteridae occupied a position in the Palaeodictyoptera not far from the stock which produced the Plectoptera [= Ephemeroptera]." We would agree with Carpenter although we would note that the wings of the Syntonopteridae have no features which would preclude their inclusion among the Ephemeroptera.[6] The Palaeodictyoptera are characterized by having two cerci, while the mayflies have two cerci *plus* a median filament (although this is greatly reduced in about half the extant families); the number of caudal filaments of the Syntonopteridae is unknown. The point seems minor, but may be fundamental. If we accept the belief that Machiloid-like Thysanura were ancestral to the winged insects, then it seems likely that the first winged insects would agree with their thysanuran ancestors in having three caudal filaments. We suspect not only that the Syntonopteridae might have had three caudal filaments but that possibly they were true Ephemeroptera. We are also inclined to suspect that further discoveries of fossils of primitive winged insects might lead to the conclusion that the Palaeodictoptera themselves represent a specialized offshoot from the Ephemeroptera rather than being ancestral to them.

Although the mayflies are generally considered to be the most primitive of winged insects, most workers have considered the fluting and intercalaries of the mayfly wing to represent specializations rather than a primitive condition. Tillyard (1932: 105), however, is inclined to regard the wing venation of mayflies as the most primitive of all insects, both fossil and recent, but, of course, the wings of the fossil genus *Lithoneura* were unknown to him.

Tillyard (op. cit.: 102) seriously questioned, but did not completely reject, the view of Martynov (1923) that the Dictyoneuridae and the genus *Triplosoba* (Protephemeridea) (Fig. 10) were the ancestors of the mayflies. While *Triplosoba* has the general facies of a mayfly, has three caudal filaments, and has retained the complete alternation of concave and convex longitudinal veins, the simple condition of MA[7] and the backward slanting of all the branches of Rs behind R_2 so as to form a somewhat pectinate Rs show specializations toward the sculling type of flight. There are, in our opinion, no members of the modern mayfly fauna that give any indication of having arisen from the Protephemeridea as represented by *Triplosoba*. Tillyard (loc. cit.) suggests that the Prote-

[6] Our judgment of the phylogenetic position of the Syntonopteridae is based primarily upon the fossils of *Lithoneura* rather than upon the fragment of the wing of *Syntonoptera*.

[7] The original figure of the wings of *Triplosoba* by Brongniart (1893) shows MA arising from R_1 rather than from MP as in the subsequent figures published by Handlirsch (1908) and Tillyard (1932).

phemeridea represent a side branch not in the direct ancestral line of the true Ephemeroptera, and Needham (1935b: 207) and Martynov (1938) have indicated a similar position for this form. As *Triplosoba* has three tails present, the cerci plus a median filament, a condition shared with the true mayflies of the Permian, it would seem likely that if we are correct in assuming a common ancestry for *Triplosoba* and the Syntonopteridae, the latter may, as we have remarked above, prove to have three tails, when and if specimens are found with these structures preserved. The position of the Dictyoneuridae would seem to be even more remote from the ancestral stock of the mayflies.

Tillyard (op. cit.) has discussed at length the possibilities concerning the relationships of the Permain Protereismatidae and Misthodotidae to modern mayflies. While he draws no definite conclusions as to which family gave rise to Recent forms, he states that the evidence favors the Protereismatidae. He seems concerned about his failure to demonstrate the presence of the CuA triad of Protereismatidae (Figs. 11, 12) in extant mayflies. The CuA of the forewing of most Siphlonuridae (Fig. 1) is so similar to the same vein in the hind wings of some species of *Protereisma* (Fig. 11) that it is difficult to understand Tillyard's concern on this point. Indeed, the CuA triad can be detected in most modern genera of mayflies and is very well developed in some Ephemeroidea.

Tillyard noted that the otherwise primitive wing of *Baetisca* (Fig. 13) shows no sign of a triad on CuA. *Baetisca* and its somewhat aberrant relative, *Prosopistoma*, have long been recognized as being markedly distinct from the remainder of the mayflies. The wings of *Baetisca* are so fundamentally similar to those of Permian family Misthodotidae (Fig. 14), which likewise lacked the cubital triad, that it would seem most logical to account for the distinctness of *Baetisca* and *Prosopistoma* by assuming that they originated from the Misthodotidae or some misthodotid-like group. On the basis of their cubital veins all the remaining mayflies probably arose from the Protereismatidae or some protereismatid-like form, although it is possible that the Palingeniopsidae or some related form gave rise to the burrowing mayflies (Ephemeroidea).

VENATIONAL NOMENCLATURE OF THE MAYFLIES

At the present time there is some dispute over the nomenclature and homologies of veins of the mayfly wing. The history of the venational nomenclature of the mayflies has been adequately reviewed in several publications (Tillyard, 1932; Spieth, 1933; and Needham, 1935b) so the treatment here will be limited to a discussion of the identity of the vein variously called MA or R_4 and R_5. In 1923, Tillyard proposed a system of nomenclature based on studies of fossil forms, and adults and nymphal wing pad development of some primitive modern genera. At this time he had not yet seen the paper by Lameere (1922) in which it was recognized for the first time that the media was composed of two parts, an anterior convex and a posterior concave element. In 1926, Tillyard modified his earlier system by recognizing the median anterior vein (MA) of Lameere. He again modified the system slightly in 1932 to make the venational symbols coincide with the Comstock-Needham system.

Needham (1935b) concludes that MA is not represented in the mayfly wing. He therefore proposed a nomenclature which is somewhat similar to Tillyard's (1923), but he made several small, yet significant, changes. Forbes (1943) reviewed the problem again and accepted the Needham nomenclature except that he refers to the Cu_2 of Needham as the plical vein.

At the present time both the Needham system of 1935 and the Tillyard nomenclature of 1932 are in common usage. There is but a single major point of disagreement between the two aforementioned systems, namely: Is the convex vein which lies between the concave radial sector and the concave media part of the radial sector or is it media anterior (MA)?

From the previous discussion it is obvious that the Tillyard system of 1932 has been accepted in this paper. His interpretations appear to be correct and are given support by two new evidences: (1) the discovery and description of the two fossil species of Syntonopteridae, *Lithoneura mirifica* and *L. lameeri*, and clarification of the position of *Syntonoptera* by Carpenter (1938, 1944); and (2) the present work on the mechanics of flight of mayflies.

The wings of the family Syntonopteridae are remarkably primitive and very similar to the archetype venation herein proposed. Radial sector is five-branched as the result of the formation of a triad on R_3. In the genus *Syntonoptera* MA is entirely free from Rs although it does arch toward it basally. In the wing of *Lithoneura mirifica* Carpenter (described from Mazon Creek, Illinois, Upper Carboniferous formation)

MA branches anteriorly, fuses for a short distance with the base of Rs and then continues as a convex vein.

In comparing members of the pre-mayfly family Syntonopteridae with the Permian mayflies of the family Protereismatidae (figs. 11 and 12) only a few differences are evident. In the latter a few veins have different courses, the forks are deeper, and R_4 and R_5 are fused. The main point of interest here is that MA is *still attached to MP basally but arches forward as in Lithoneura* to fuse with Rs for a short distance before continuing on as a convex vein. Tillyard (1932) pointed out the evidence of this fusion in *Protereisma*, but it is much more pronounced in *Lithoneura*.

The essential difference between the venation of the Permian *Protereisma* and the modern Siphlonuridae is that the basal connection of MA to MP has been lost and MA appears to arise from Rs. Actually, in the Recent genera studied in the present work, the bases of Rs and MA are independent and merely abut against one another.

The fact that the concave or convex positions of the vein serves an important function in flight most certainly would seem to preclude the possibility of complete loss of MA and the substitution in its place of parts of Rs which would apparently have had to change from concave to convex. The function of the wing would, however, be in no way impaired by a shifting of the base of MA so that it is associated with Rs rather than MP. There thus seems to be wholly adequate evidence to show that the vein in question was originally part of media and not a part of the radial sector.

The primary evidence for the belief that the vein in question is part of Rs rather than MA has stemmed from the fact that the vein is supplied by a trachea that arises from Rs. The tracheal connections in the developing mayfly wings vary considerably as has been demonstrated by Morgan (1912) and Tillyard (1923), yet the adult wing venation illustrates considerable conservatism. The relative stability of the venation has been imposed by the mechanical needs of the wing, each variation that interfered with the mechanics of flight being eliminated. While the tracheation of the mayfly wing apparently has played an important part in the phylogenetic development of venation, it most certainly does not have enough stability in nymphal mayflies to justify its use in maintaining a venational nomenclature contrary to the evidence from the fossil record. As Needham (1951) has so aptly pointed out, tracheal evidences are valuable only when used judiciously and with caution. It is possible that the small callus or sclerotized plate in the developing nymphal wing pad of Ephemeroptera may have played a role in uniting MA to the base of Rs, but this reasoning apparently would not apply to the other insect groups where MA has fused with Rs.

ACKNOWLEDGMENTS

We are deeply indebted to several persons who have aided us during the present study. Dr. C. P. Alexander (University of Massachusetts) made many helpful suggestions during the investigations and writing of this work. Dr. F. M. Carpenter (Harvard University) and Dr. H. T. Spieth (University of California, Riverside) critically reviewed early drafts of the manuscript but did not necessarily agree with all parts of the paper. Dr. Herbert H. Ross (Illinois Natural History Survey) and Dr. Georges Demoulin (Institut Royal des Sciences Naturelles de Belgique) have read the final manuscript and have made a number of valuable suggestions. Dr. Dan McLachlan, Jr. (University of Utah), has aided in the interpretation of the physics of flight mechanics. To these and many others who, through their constructive criticism, have aided this investigation, we offer our warmest thanks.

LITERATURE CITED

ADOLPH, G. E. *Ueber Insektenflügel.* Nova Acta Leop.-Carol. deutschen Akad. Naturf. **41**: 215–291, pls. 27–32. 1879.

BERNER, L. Baetisca rogersi, *a new mayfly from northern Florida.* Can. Ent. **72**: 156–160, 5 figs. 1940.

BRADLEY, J. C. *A laboratory guide to the study of the wings of insects:* 41 pp. Ithaca, N. Y., 1931.

BRONGNIART, C. *Recherches pour servir à l'histoire des insectes fossiles des temps primaires précédées d'une étude sur la nervation des ailes insectes.* Industrie Minérale, ser. 3, **7**: 1893.

CARPENTER, F. M. *Two Carboniferous insects from the vicinity of Mazon Creek, Illinois.* Amer. Journ. Sci. **36**: 445–452, 3 figs. 1938.

———. *Carboniferous insects from the vicinity of Mazon Creek, Illinois.* Illinois State Mus. Sci. Papers 3: 20 pp., 5 figs, 4 pls. 1944.

COMSTOCK, J. H. *The wings of insects.* Ithaca, N. Y., 1918.

COMSTOCK, J. H., and J. G. NEEDHAM. *The wings of insects.* Amer. Nat. **33**: 117–126. 1898.

FORBES, W. T. M. *The origin of wings and venational types in insects.* Amer. Midl. Nat. **29**: 381–405, 10 figs. 1943.

HANDLIRSCH, A. *Die fossilen Insekten und die Phylogenie der rezenten Formen*. Leipzig, 1908.

LAMEERE, A. *Étude sur l'évolution des éphémères*. Bull. Soc. Zool. France **42**: 41–59, 61–81. 1917.

———. *Sur le nervation alaire des insectes*. Bull. Classe Sci. Acad. Roy. Belgique, sér. 5, **8**: 38–149. 1922.

MARTYNOV, A. B. *The interpretation of the wing venation and tracheation of the Odonata and Agnatha*. Rev. Russe Ent. **18**: 145–174, 3 figs., 1 pl. 1923. (Translation in Psyche **37**: 245–281. 1931.)

———. *Études sur l'histoire géologique et de phylogénie des ordres des insectes ptérygotes*. Trav. Inst. Paleontol., Acad. Sci. U.R.S.S., **7**(4): 1–150, 1 pl., 70 figs. 1938.

MORGAN, A. H. *Homologies in the wing veins of mayflies*. Ann. Ent. Soc. Amer. **5**: 89–106, pls. 5–9. 1912.

NEEDHAM, J. G. *Some basic principles of insect wing venation*. Journ. New York Ent. Soc. **43**: 113–129. 1935a.

———. *In* Needham, Traver, and Hsu. *The biology of mayflies*. Ithaca, N. Y., 1935b.

———. *Prodrome for manual of the dragonflies of North America, with extended comments on wing venation systems*. Trans. Amer. Ent. Soc. **77**: 21–62, 7 text figs., 5 pl. 1951.

SIMPSON, G. G. *The meaning of evolution*. New Haven, 1950.

SNODGRASS, R. E. *Principles of insect morphology*. New York and London, 1935.

SPIETH, H. T. *The phylogeny of some mayfly genera*. Journ. New York Ent. Soc. **41**: 55–86, 327–390, pls. 16–24. 1933.

TILLYARD, R. J. *The panorpoid complex. Part 3: The wing venation*. Proc. Linn. Soc. New South Wales **44**: 533–718, pls. 31–35, figs. 35–112. 1919.

———. *The wing venation of the order Plectoptera or mayflies*. Journ. Linn. Soc. London, Zool., **35**: 143–162, text figs. 1–10. 1923.

———. *The insects of Australia and New Zealand*. Sydney, 1926.

———. *Kansas Permian insects, Pt. 15. The order Plectoptera*. Amer. Journ. Sci. **23**: 97–134, 237–272, 22 text figs. 1932.

HERPETOLOGY.—*Description of a new frog of the genus* Eleutherodactylus *from Jamaica, B.W.I.*

W. GARDNER LYNN,[1] Catholic University of America.

In 1943 Lynn and Dent, in discussing the distribution of the Jamaican frog *Eleutherodactylus cundalli* Dunn, presented a new locality record as follows: "The present collections . . . provide the first record of its occurrence on the south coast. It is the only frog occurring on the hot dry limestones of Portland Ridge. Here it was found in deep caves, presumably the only places where there is sufficient moisture to enable it to survive. The cave specimens are very light gray in color, quite large in size and have a very tender skin that usually tears when the animals are captured."

This record was based on eight specimens taken in two different caves on Portland Ridge on August 19, 1941. Since that time C. B. Lewis, of the Institute of Jamaica, has collected six more specimens on various trips to the region, and the present author, during a year spent in Jamaica (July 1952–September 1953) took 19 specimens in the course of seven visits to the caves. Study of this new material shows that the cave specimens represent a species which, though clearly related to *E. cundalli*, is quite distinct. Portland Ridge is a hilly limestone peninsula projecting into the sea from the south coast of Jamaica, connected with the main body of the island by a marshy plain. As Grant (1940) has pointed out it constitutes a sort of "biological island" with a certain degree of endemism in its fauna. It is therefore not surprising that the only *Eleutherodactylus* taken in the area proves to be distinct from other Jamaican forms.

Eleutherodactylus cavernicola, n. sp. (Fig. 1)

Type.—U. S. Nat. Mus. no. 135239, an adult female from Portland Cave, Clarendon Parish, Jamaica, B.W.I., collected June 28, 1953, by W. G. Lynn.

Paratypes.—U. S. Nat. Mus. nos. 117737–117744, collected August 19, 1941, by J. N. Dent and W. G. Lynn; U. S. Nat. Mus. nos. 135240–135257, collected October 24, 1952, to July 28, 1953, by W. G. Lynn; Museum of the

[1] Most of the material upon which this paper is based was collected by the author during the period from July 1952 to September 1953. During the summer of 1952 the work was aided by a grant from the National Science Foundation. Collections through the rest of the period were made during the author's tenure as a Fulbright Scholar at the University College of the West Indies. My gratitude is due to C. Bernard Lewis, director of the Science Museum of the Institute of Jamaica, for making available specimens collected by him and for guiding me to most of the caves visited.

Institute of Jamaica nos. 1943. 1, 1943. 2, collected April 20, 1943, by C. B. Lewis; Museum of the Institute of Jamaica nos. 1952. 8–1952.10, collected January 10, 1952, by C. B. Lewis. All the paratypes are from caverns on Portland Ridge within 4 miles of the type locality.

Diagnosis.—Resembles *Eleutherodactylus cundalli* Dunn in most characters but differs in having shorter hind limbs and a greater adult body size, and in the absence of any striking sexual dimorphism in the size of the tympanum.

Description of type.—Vomerine teeth in two long series extending laterally beyond the level of the choanae and converging backward medially; tongue oval, not deeply notched, free behind; greatest width of tongue two-thirds that of mouth opening; snout truncated as seen from above or in profile; upper jaw projecting beyond lower; nostrils lateral in position, much nearer to tip of snout than to eye; loreal region concave; diameter of eye equal to distance from eye to nostril; upper eyelid nearly as wide as interorbital space; eyelid with several small white tubercles; no ridges on head; no apparent subgular fold; diameter of tympanum one-half that of eye, separated from eye by a distance about one-half its own diameter; disks of two outer fingers enlarged, that of the second finger covering about one-third of the tympanum; disks of two inner fingers, and those of toes, small; first finger somewhat shorter than second; second finger shorter than fourth; no webs between fingers or toes; third toe slightly longer than fifth; subarticular tubercles well developed; two metatarsal tubercles; a series of plantar tubercles corresponding to the metatarsals; no tarsal fold; heels not meeting when legs are flexed with femora held at right angles to the axis of the body; heel reaching only to posterior border of eye when hind leg is adpressed; back smooth without tubercles; belly smooth; granular glandular area on posterior surfaces of thighs below the vent.

Dimensions of type.—Tip of snout to vent, 40.5 mm; greatest width of head 15.0 mm; tip of snout to posterior edge of tympanum 14.0 mm; diameter of eye 4.5 mm; diameter of tympanum 2.5 mm; fore leg from axilla 21.5 mm; hind leg from vent to tip of longest toe 51.0 mm; hind leg from vent to heel 29.0 mm.

Colors in alcohol.—Back fawn color with an interocular bar and scattered spots of seal brown; upper surfaces of limbs fawn color; belly immaculate white; faint suffusions of seal brown on throat.

Colors in life.—The ground color of living specimens varies from light tan to coppery gray, with the interocular bar and the blotches on the back dark brown. The iris of the eye is a golden bronze with a longitudinal stripe of dark brown through the pupil. A few specimens show faint tinges of yellow in the groin.

Variation.—The 33 specimens studied show no

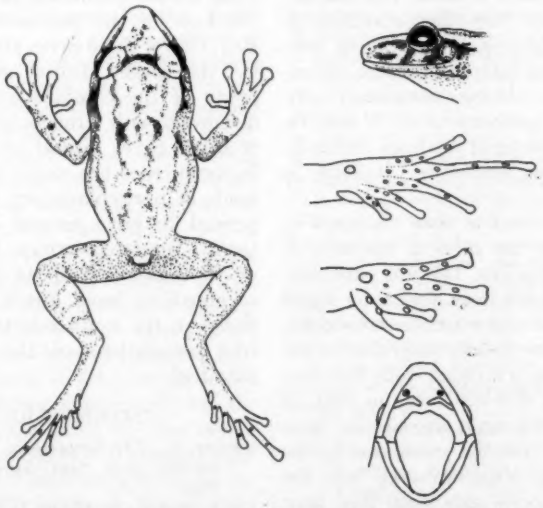


FIG. 1.—*Eleutherodactylus cavernicola*, n. sp. Sketch of dorsum and details of side of head and inside of mouth of type, ×1. Foot and hand, ×2.

significant variation in important characters. The adults range from 28.5 to 40.5 mm in length and average 33.5 mm. This is a considerably greater size than has been found in any population of *E. cundalli*. Because of the absence of any sexual dimorphism it is not possible to give a figure for average size of each sex. However, dissection of several of the largest specimens reveals that both males and females reach at least 38.0 mm. This is in contrast to *E. cundalli* in which females average about 5.0 mm longer than males.

The color pattern of all specimens accords closely with that illustrated for the type. All show a fairly well-defined interocular bar and dark lines extending over the tympanum. Aside from this the pattern consists of an irregular mottling of dark spots. It is noteworthy that no specimens exhibit the W-shaped mark in the suprascapular region, which is a common feature in *E. cundalli*, and there are no examples showing a middorsal light stripe.

Habits and habitat.—Some specimens were taken sufficiently near the entrances of the caverns to be exposed to the light, but others were found at various distances up to at least half a mile inside the caves. Most of the frogs were found on or near the floor, but on several occasions specimens were taken from among the draperylike folds of stalactites at 4–6 feet above the floor. Considering the number of collecting trips made, the total collection is small. This can not be taken to indicate that the population is sparse, however. Many of the specimens seen escaped by retreating into deep fissures. Moreover, several trips, during particularly dry periods, yielded no specimens at all. It may be assumed that at these times the frogs remain in the deeper passages where the moisture is retained.

A considerable amount of time was spent in turning rocks within the caves in the hope of finding the eggs of this frog. This was unsuccessful and, moreover, adult frogs were never found beneath rocks. In this connection it is noteworthy that there is only one juvenile individual in the entire collection. This is a rather badly shriveled specimen measuring 12.0 mm taken in 1943. It seems likely that the eggs are laid in deep, narrow fissures and that the young may prefer such situations, the frogs venturing into the larger parts of the caves only when they have reached adult size.

Whether this frog ever ranges far outside the caves is questionable. Turning rocks and logs in the region yielded small lizards and snakes but no frogs, even in the rainy season. The only other amphibian in the region is the introduced toad, *Bufo marinus*. Two adults were found near cave entrances and tadpoles were observed in the small sink hole which provides the water supply for the few families living near Jacksons Bay.

E. cavernicola, in contrast to *E. cundalli*, is a fairly vocal frog, the call consisting of a high-pitched oft-repeated chirp, which can be heard for considerable distances. Frogs were heard calling much more frequently during May to July than at other times of the year. This, together with the fact that females with large ovarian eggs were taken at this time only, probably indicates that the breeding season is limited to the summer months.

Only one of the caves of Portland Ridge is sufficiently well known to have a name. This, the Portland Cave, is marked on the road map of the Jamaica Automobile Association and is now accessible by road. It lies on the north side of the ridge within a mile of the end of Portland Point. This cave and two others in the immediate vicinity yielded most of the frogs in the collection. The others came from two caves lying on the south side of the ridge close to the base of the peninsula, near Jacksons Bay. One of these caves may be distinguished by the large vaulted entrance in which many of the columns and stalagmites are decorated with Arawak carvings. A number of other caves visited yielded no frogs but in some cases the visits were short or were made at particularly dry times. Most caves proved to have several entrances and extensive interconnections. Whether the caves of the northern tip of the point can be assumed to have direct connections with those on the south side is not clear but the frog populations of the two seem to be identical.

LITERATURE CITED

GRANT, C. *The herpetology of Jamaica II. The reptiles.* Bull. Inst. Jamaica, sci. ser. no. 1. 1940.

LYNN, W. G., and DENT, J. N. *Notes on Jamaican amphibians.* Copeia 1943: 234.

PROCEEDINGS OF THE ACADEMY

471ST MEETING OF BOARD OF MANAGERS

The 471st meeting of the Board of Managers, held in the Tayloe Room of the Cosmos Club, April 20, 1954, was called to order by the President at 8 P.M., with the following in attendance: F. M. DEFANDORF, MARGARET PITTMAN, J. R. SWALLEN, J. A. STEVENSON, J. C. EWERS, W. W. DIEHL, M. A. MASON, S. E. FORBUSH, W. A. DAYTON, J. K. TAYLOR, F. W. POOS, G. F. GRAVATT, A. H. SCOTT, J. G. THOMPSON, F. N. FRENKIEL, and, by invitation, D. J. DAVIS and MARY JEANNE KREEK.

Dr. DAVIS, Chairman of the Committee on Meetings, reported that the May meeting would be held at the Army Map Service and would include a 45-minute discussion of the Army Map Service and an opportunity to see the Niovac in operation. The October meeting would be held at the Johns Hopkins University Applied Physics Laboratory, and the November meeting jointly with the Biological Society, with Dr. Konrad Lorenz, of Germany, as the speaker. The December meeting is being arranged by Dr. Seeger. It will be a panel type of discussion on science education with Dr. Samuel H. Brownell, Commissioner of Education, as one of the leaders.

Dr. MCPHERSON presented revisions of the constitution and bylaws of the Junior Academy. After some discussion the matter was tabled until the next meeting of the Board. A proposal was made to publish a Red Book of the Junior Academy. This could be financed by the Junior Academy if distribution were only to members of the Junior Academy, but if sent to all members of the Washington Academy as well some assistance would be needed. The Board requested that plans and estimates be made by the Junior Academy to be presented at the next meeting. Dr. McPherson said that if any funds were left from the Science Fair they would be used to send Keith Johnson to the National Science Fair at Purdue University. It was estimated that the cost of the Science Fair would be about $1,100. Mention was made of the economies effected by Mr. Johnson in planning the fair, especially the electric wiring which can be used year after year.

MARY JEANNE KREEK, on behalf of the Junior Academy, expressed her appreciation for the interest and assistance given by the senior Academy, especially in regard to the Science Fair.

President Defandorf read the minutes of the first meeting of the Committee on Science Education held on April 5:

The following people attended the first meeting of the Washington Academy of Sciences Committee on Science Education at the National Science Foundation on April 5 at 8 p.m.: RONALD BAMFORD, R. PERCY BARNES, GEORGE D. ROCK, B. D. VAN EVERA, and RAYMOND J. SEEGER, Chairman. The following individuals had indicated that they were unable to be present: WALLACE R. BRODE, HUGH L. DRYDEN, MARTIN A. MASON, WILLIAM H. SEBRELL, WALDO L. SCHMITT, WILLIAM E. WRATHER. In addition, the following were absent: CLIFFORD A. BETTS, LEONARD CARMICHAEL, and WILLIAM W. RUBEY.

There was general discussion as to what might be the most strategic functioning of the Committee. The Chairman emphasized the breadth of the problem. In the first place one might be concerned with curricula for the following: (1) General education in science for potential nonscientists and (2) special education for potential scientists. Secondly, one might consider the objectives and techniques for developing scientists from the following points of view: (1) the institutional sources of science teachers with due regard to curricula offerings and State requirements, (2) science implementation for active teachers (3) conferences with administrators (supervisors, principals, superintendents) responsible for the administration of science, and finally, (4) conferences with Boards of Education responsible for policies in science education.

It was generally agreed that the starting point of the Committee should be the well-known manpower need for scientists. The United States Office of Education figures for the past eight years indicate clearly that whereas the number of graduates at the baccalaureate level has increased 50 percent, there has been at best a constant level of graduates in the sciences (in some instances actually a decline). The questions generally are: What are the factors that are contributing to this state of affairs? How can the present situation be improved? Specifically, in what ways can the Washington Academy of Sciences be of assistance in solving the local problems?

It was agreed that the Chairman of the Committee might make contacts with the other State Academies of Sciences, particularly those in Maryland and Virginia, in order to ascertain whether any cooperative effort might be achieved for these States and whether any information might be available from other State Academies of Sciences as to their interest in this activity.

It was further agreed that there should be a meeting of the Committee with each of the following groups:

(1) Science supervisors in District of Columbia, Montgomery County, Prince Georges County, Arlington County, and Fairfax County.
(2) Professors of science education from the local universities.

(3) Local superintendents of education.

It was expected that only one of these meetings can be held this spring, namely, the one with the science supervisors. It is scheduled for 8 p.m. on May 25 in the Board Room of the National Science Foundation, 1520 H Street, NW.

It was further planned to devote one of the meetings of the Washington Academy of Sciences, possibly that of November 18, to a panel discussion of the general problem (the Commissioner of Education of the United States and the President of the National Academy of Sciences were suggested as possible participants).

The Chairman called attention to the following material for study in connection with the working material. In so far as possible he will try to obtain a copy of the public documents for each member of the Committee.

Education Policies Commission, N.E.A.: "Education of the Gifted" (1950)

U. S. Office of Education: "Mathematics in Public High Schools" (Bulletin 1953, No. 5)

U. S. Office of Education: "The Teaching of Sciences in Public High Schools" (Bulletin 1950, No. 9)

Carnegie Corporation of New York Conference at Harvard: "Critical Years Ahead in Science Teaching" (1953)

Following a reading of this report, the Board approved a special allotment of $75 for expenses of the newly formed Committee on Science Education, as no provision had been made for expenses of this Committee when the 1954 budget was adopted.

The Secretary reported the results of the ballot vote on the affiliation of the District of Columbia Branch of the American Meteorological Society. Of the 321 votes cast, 320 were for affiliation and 1 against. Dr. FRANCIS W. REICHELDERFER, nominated for Vice-President representing the newly affiliated society, was elected by the Board.

President DEFANDORF presented statistics on the financial status of the Academy, particularly in relation to the JOURNAL, with the purpose of stimulating ideas "for improving and expanding the Academy's base of operations." These data showed that 85 percent of the income of the Academy was used for publication of the JOURNAL. After a rather extended discussion, Dr. Mason suggested that the Committee on Policy and Planning be given assistance with the request that they examine the total activities of the Academy, particularly in respect to the JOURNAL. A motion that the President appoint a special committee of six or so members for this study was unanimously carried.

472D MEETING OF BOARD OF MANAGERS

The 472d meeting of the Board of Managers, held in the Tayloe Room of the Cosmos Club, May 18, 1954, was called to order by the President at 8 P.M. with the following in attendance: F. M. DEFANDORF, MARGARET PITTMAN, J. R. SWALLEN, H. S. RAPPLEYE, J. A. STEVENSON, J. C. EWERS, A. T. MCPHERSON, A. B. GURNEY, S. E. FORBUSH, G. F. GRAVATT, C. A. BETTS, GLEN SLOCUM, R. S. DILL, F. W. REICHELDERFER, and, by invitation, HEINZ SPECHT, H. N. EATON, and KEITH JOHNSON.

Dr. MCPHERSON again presented the revised constitution and bylaws of the Junior Academy. After commenting on some of the changes, he moved that the new constitution and bylaws be adopted. The motion was carried unanimously. A prospectus or dummy of the Red Book of the Junior Academy was presented, as well as estimates for printing based on 500 copies for the Junior Academy and 1,500 copies if the Academy wanted them for distribution. Printing of 1,500 copies was approved, the senior Academy to bear the expense of the additional copies. The distribution of these copies was left to the discretion of the Committee on Encouragement of Science Talent.

KEITH JOHNSON gave a report on the Science Fair. Fifty-five schools participated, 10 more than last year. There were 952 exhibits, of which 258 were from the seventh grade, 402 from the eighth and ninth grades, and 292 from senior high school. In all, 105 judges participated, and 300 student awards were given. Plaques were presented to 10 schools in special recognition for their work in the Fair. Two students were sent to the National Science Fair at Purdue University, and one of whom placed among the upper five.

The Secretary read a letter from CHARLES F. SWINGLE requesting that he be placed on the retired list. Having paid dues for 19 years, the request was approved, effective December 30, 1953.

JASON R. SWALLEN, *Secretary.*

INDEX TO VOLUME 44

PROCEEDINGS OF THE ACADEMY AND AFFILIATED SOCIETIES

Anthropological Society of Washington. 94.
Washington Academy of Sciences. 59, 157, 374, 403.

AUTHOR INDEX

ABRAMOWITZ, MILTON. See ANTOSIEWICZ, H. A. 382.

ANTOSIEWICZ, H. A., and ABRAMOWITZ, MILTON. A representation for solutions of analytic systems of linear differential equations. 382.

BAKELESS, JOHN E. Lewis and Clark's background for exploration. 334.

BAKER, M., and ERICKSEN, J. L. Inequalities restricting the form of the stress-deformation relations for isotropic elastic solids and Reiner-Rivlin fluids. 33.

BAYER, FREDERICK M. New names for two genera of Octocorallia. 296.

BETHE, HANS A. Mesons and nuclear forces. 97.

BLAKE, DORIS H. Five new species of chrysomelid beetles. 246.

CAMPAIGNE, HOWARD H. A lower limit on the number of hypergroups of a given order. 5.

CASEY, RAYMOND. New genera and subgenera of Lower Cretaceous ammonites. 106.

CASH, EDITH K. Some Discomycetes new to Alaska. 44.

CHACE, FENNER A., Jr. Two new subterranean shrimps (Decapoda: Caridea) from Florida and the West Indies, with a revised key to the American species. 318.

CLARK, AUSTIN H. For and against the doctrine of prescription as applied to taxonomy: A historical retrospect. 13.

COE, WESLEY R. Geographical distribution and means of dispersal of the bathypelagic nemerteans found in the great submarine canyon at Monterey Bay, California. 324.

DAYTON, WILLIAM A. Some more notes on American ashes (*Fraxinus*). 385.

DEIGNAN, H. G. Five new races of bulbuls (Pycnonitidae) from southern Asia. 123.

DOWNS, ROBERT J. See SMITH, LYMAN B. 311.

DRAKE, CARL J. New Saldidae (Hemiptera) from the Old World. 194.

DRECHSLER, CHARLES. A nematode-capturing fungus with clamp-connections and curved conidia. 82.

———. *Aphanomyces euteiches* from pea roots and "*Aphanomyces euteiches* P. F. 2." 236.

———. Morphological features shown in *Aphanomyces* isolations from roots of spinach and flax. 212.

EDMUNDS, GEORGE F., Jr., and TRAVER, JAY R. The flight mechanics and evolution of the wings of Ephemeroptera, with notes on the archetype insect wing. 390.

ERICKSEN, J. L. See BAKER, M. 33.

FAHRENBACH, WOLF-HENRICH. A new species of the genus *Diarthrodes* (Crustacea, Copepoda) parasitic in a red alga. 326.

FERLIN, H. J., and KARABINOS, J. V. Differential media for *Escherichia coli* and *Aerobacter aerogenes*. 303.

FORCART, LOTHAR. *Leiostracus* (?) *kugleri*, n. sp., a new bulimulid mollusk from Venezuela. 58.

FRIIS, HERMAN R. Cartographic and geographic activities of the Lewis and Clark expedition. 338.

GINSBURG, ISAAC. Four new fishes and one little-known species from the east coast of the United States including the Gulf of Mexico. 256.

HARTMAN, OLGA. New species of polychaetous worms from the Marianas and Gilbert Islands. 228.

HOFFMAN, RICHARD L. Further studies on American millipeds of the family Euryuridae (Polydesmida). 49.

INGER, ROBERT F. On a collection of amphibians from Mount Kina Balu, North Borneo. 250.

IRVING, LAURENCE, and PANEAK, SIMON. Biological reconnaissance along the Ahlasuruk River east of Howard Pass, Brooks Range, Alaska, with notes on the avifauna. 201.

JOHNSON, PHYLLIS T. Notes on *Pleochaetis* Jordan, 1933, from Colombia, with the description of a new species (Siphonaptera: Ceratophyllidae). 289.

KARABINOS, J. V. See FERLIN, H. J. 303.

KEHOE, THOMAS F. Stone "medicine wheels" in southern Alberta and the adjacent portion of Montana: Were they designed as grave markers? 133.

LI, HUI-LIN. Trapellaceae, a familial segregate from the Asiatic flora. 11.

LOEBLICH, ALFRED R., Jr., and TAPPAN, HELEN. Emendation of the foraminiferal genera *Ammodiscus* Reuss, 1862, and *Involutina* Terquem, 1862. 306.

———. New names for two foraminiferal homonyms. 384.

LURIE, NANCY OESTREICH. See RAY, VERNE E. 358.

LYNN, W. GARDNER. Description of a new frog of the genus *Eleutherodactylus* from Jamaica, B.W.I. 400.

MAHAN, A. I. Some newly solved and some unsolved problems in optics. 165.
MAMAY, SERGIUS H. A Permian *Discinites* cone. 7
MARGENAU, HENRY. Advantages and disadvantages of various interpretations of the quantum theory. 265.
MATTOX, N. T. Description of *Eocyzicus concavus* (Mackin) with a review of other North American species of the genus (Crustacea: Conchostraca). 46.
McDERMOTT, JOHN FRANCIS. William Clark: Pioneer museum man. 370.
MORRISON, J. P. E. *Hydrobia totteni*, new name for *Turbo minuta* Totten, 1834 (Gastropoda: Hydrobiidae). 26.
NICOL, DAVID Trends and problems in pelecypod classification (the supergeneric categories). 27.
NOLAN, M. O., and VON BRAND, THEODOR. The weight relations between shell and soft tissues during the growth of some fresh-water snails. 251.
OBRAZTSOV, NICHOLAS S. Notes on some species of the *Amata* (*Syntomis*) *cymatilis* group from the Philippine Islands, with description of a new species (Lepidoptera: Ctenuchidae). 221.
PANEAK, SIMON. See IRVING, LAURENCE. 201.
PARKES, KENNETH C. See WETMORE, ALEXANDER. 126.
RAY, VERNE F., and LURIE, NANCY OESTREICH. The contributions of Lewis and Clark to ethnography. 358.
ROSENTHAL, JENNY E. Critical appraisal of the validity of standard techniques of conformal mapping. 276.
ROSSO, SAMUEL W. A study of the shell structure and mantle epithelium of *Musculium transversum* (Say). 329.
RUDD, VELVA E. Botanical contributions of the Lewis and Clark expedition. 351.
———. *Centrolobium* (Leguminosae): Validation of a specific name and a brief review of the genus. 284.
SEBASTIAN, V. O. On *Polyclinum indicum*, a new ascidian from the Madras coast of India. 18.
SEEGER, RAYMOND J. On research and education —in fluid dynamics. 1.
SETZER, HENRY W. Zoological contributions of the Lewis and Clark expedition. 356.
SILSBEE, F. B. Paul Gough Agnew (obituary). 95.
SINGH, KUNWAR SURESH. *Psilocollaris indicus*, n. gen., n. sp. (Psilostomidae Odhner, 1911: Trematoda) from an Indian stork, *Dissura e. episcopus*. 24.
SMITH, LYMAN B., and DOWNS, ROBERT J. Xyridaceae from Brazil. 311.
SOHNS, ERNEST R. *Setaria:* Fascicle organization in four species. 116.
SPILMAN, T. J. Generic names of the Salpingidae and their type species (Coleoptera). 85.
STRIMPLE, HARRELL L. Two new crinoid species from the Henryhouse of Oklahoma. 280.
TAPPAN, HELEN. See LOEBLICH, ALFRED R., Jr. 306, 384.
THURMAN, DEED C., Jr. *Ayurakitia*, a new genus of mosquito from northern Thailand (Diptera: Culicidae). 197.
TODD, JOHN. Experiments in the solution of differential equations by Monte Carlo methods. 377.
TRAVER, JAY R. See EDMUNDS, GEORGE F. 390.
TRESSLER, WILLIS L. Fresh-water Ostracoda from Texas and Mexico. 138.
VENNING, FRANK D. The reciprocal effects between calcium and phosphate ions upon the growth, composition, and structure of castor bean, *Ricinus communis* L. 65.
VOKES, H. E. On the pelecypod genus *Platopis* Whitfield: III. 137.
———. Some primitive fossil pelecypods and their possible significance. 233.
———. The development of the hinge of *Veniella conradi* (Morton) and some conclusions based on its study. 36.
VON BRAND, THEODOR. See NOLAN, M. O. 251.
WALKLEY, LUELLA M. A new cryptine genus of economic interest (Hymenoptera: Ichneumonidae). 219.
WETMORE, ALEXANDER, and PARKES, KENNETH C. Notes on the generic affiliations of the great grebe of South America. 126.
WHARTON, G. W. Observations on the feeding of prostigmatid larvae (Acarina: Trombidiformes) on arthropods. 244.
WHEELER, GEORGE C., and WHEELER, JEANETTE. The ant larvae of the myrmicine tribes Cataulacini and Cephalotini. 149.
WILLIAMSON, A. A. Integration and individuation as elements in evolution. 297.
WITTMER, W. New Cantharidae (Coleoptera) from the collection of the United States National Museum. 314.

SUBJECT INDEX

Anthropology. Stone "medicine wheels" in southern Alberta and the adjacent portion of Montana: Were they designed as grave markers? THOMAS F. KEHOE. 133.

Biochemistry. Differential media for *Escherichia coli* and *Aerobacter aerogenes*. H. J. FERLIN and J. V. KARABINOS. 303.

The reciprocal effects between calcium and phosphate ions upon the growth, composition, and structure of castor bean, *Ricinus communis* L. FRANK D. VENNING. 65.

Biography. Portraits of Lewis and Clark. 333.

William Clark: Pioneer museum man. JOHN FRANCIS MCDERMOTT. 370.

Biology. Biological reconnaissance along the Ahlasuruk River east of Howard Pass, Brooks Range, Alaska, with notes on the avifauna. LAURENCE IRVING and SIMON PANEAK. 201.

Integration and individuation as elements in evolution. A. A. WILLIAMSON. 297.

Botany. Botanical contributions of the Lewis and Clark expedition. VELVA E. RUDD. 351.

Centrolobium (Leguminosae): Validation of a specific name and a brief review of the genus. VELVA E. RUDD. 284.

Setaria: Fascicle organization in four species. ERNEST R. SOHNS. 116.

Some more notes on United States ashes (*Fraxinus*). WILLIAM A. DAYTON. 385.

Trapellaceae, a familial segregate from the Asiatic flora. HUI-LIN LI. 11.

Xyridaceae from Brazil. LYMAN B. SMITH and ROBERT J. DOWNS. 311.

Cartography. Cartographic and geographic activities of the Lewis and Clark expedition. HERMAN R. FRIIS. 338.

Entomology. A new cryptine genus of economic interest (Hymenoptera: Ichneumonidae). LUELLA M. WALKLEY. 219.

Ayurakitia, a new genus of mosquito from northern Thailand (Diptera: Culicidae). DEED C. THURMAN, Jr. 197.

Five new species of chrysomelid beetles. DORIS H. BLAKE. 246.

Generic names of the Salpingidae and their type species (Coleoptera). T. J. SPILMAN. 85.

New Cantharidae (Coleoptera) from the collection of the United States National Museum. W. WITTMER. 314.

New Saldidae (Hemiptera) from the Old World. CARL J. DRAKE. 194.

Notes on *Pleochaetis* Jordan, 1933, from Colombia, with the description of a new species (Siphonaptera: Ceratophyllidae). PHYLLIS T. JOHNSON. 289.

Notes on some species of the *Amata* (*Syntomis*) *cymatilis* group from the Philippine Islands, with description of a new species (Lepidoptera: Ctenuchidae). NICHOLAS S. OBRAZTSOV. 221.

The ant larvae of the myrmicine tribes Cataulacini and Cephalotini. GEORGE C. WHEELER and JEANETTE WHEELER. 149.

The flight mechanics and evolution of the wings of Ephemeroptera, with notes on the archetype insect wing. GEORGE F. EDMUNDS, Jr., and JAY R. TRAVER. 390.

Ethnography. The contributions of Lewis and Clark to ethnography. VERNE F. RAY and NANCY OESTREICH LURIE. 358.

Exploration. Lewis and Clark's background for exploration. JOHN E. BAKELESS. 334.

Geography. Cartographic and geographic activities of the Lewis and Clark expedition. HERMAN R. FRIIS. 338.

Helminthology. *Psilocollaris indicus*, n. gen., n. sp. (Psilostomidae Odhner, 1911: Trematoda) from an Indian stork, *Dissoura e. episcopus*. KUNWAR SURESH SINGH. 24.

Herpetology. Description of a new frog of the genus *Eleutherodactylus* from Jamaica, B.W.I. W. GARDNER LYNN. 400.

On a collection of amphibians from Mount Kina Balu, North Borneo. ROBERT F. INGER. 250.

Ichthyology. Four new fishes and one little-known species from the east coast of the United States including the Gulf of Mexico. ISAAC GINSBURG. 256.

Lewis and Clark Anniversary Number. 333.

Malacology. A study of the shell structure and mantle epithelium of *Musculium transversum* (Say). SAMUEL W. ROSSO. 329.

Hydrobia totteni, a new name for *Turbo minuta* Totten, 1834 (Gastropoda: Hydrobiidae). J. P. E. MORRISON. 26.

Leiostracus (?) *kugleri*, n. sp., a new bulimulid mollusk from Venezuela. LOTHAR FORCART. 58.

The weight relations between shell and soft tissues during the growth of some fresh water snails. M. O. NOLAN and THEODOR VON BRAND. 251.

Trends and problems in pelecypod classification (the supergeneric categories). DAVID NICOL. 27.

Mathematics. A lower limit on the number of hypergroups of a given order. HOWARD H. CAMPAIGNE. 5.

A representation for solutions of analytic systems of linear differential equations. H. A. ANTOSIEWICZ and MILTON ABRAMOWITZ. 382.

Critical appraisal of the validity of standard techniques of conformal mapping. JENNY E. ROSENTHAL. 276.

Experiments in the solution of differential equations by Monte Carlo methods. JOHN TODD. 377.

Inequalities restricting the form of the stress-deformation relations for isotropic solids and Reiner-Rivlin fluids. M. BAKER and J. L. ERICKSEN. 33.

Mycology. A nematode-capturing fungus with clamp-connections and curved conidia. CHARLES DRECHSLER. 82.

Aphanomyces euteiches from pea roots and "*Aphanomyces euteiches* P. F. 2." CHARLES DRESCHLER. 236.

Morphological features shown in *Aphanomyces* isolations from roots of spinach and flax. CHARLES DRESCHLER. 212.

Some Discomycetes new to Alaska. EDITH K. CASH. 44.

New members of the Academy. 128.

Obituary. PAUL GOUGH AGNEW. 95.

Ornithology. Five new races of bulbuls (Pycnonotidae) from southern Asia. H. G. DEIGNAN. 123.

Notes on the generic affiliations of the great grebe of South America. ALEXANDER WETMORE and KENNETH C. PARKES. 126.

Paleobotany. A Permian *Discinites* cone. SERGIUS H. MAMAY. 7.

Paleontology. Emendation of the foraminiferal genera *Ammodiscus* Reuss, 1862, and *Involutina* Terquem, 1862. ALFRED R. LOEBLICH, Jr., and HELEN TAPPAN. 306.

New genera and subgenera of Lower Cretaceous ammonites. RAYMOND CASEY. 106.

New names for two foraminiferal homonyms. ALFRED R. LOEBLICH, Jr., and HELEN TAPPAN. 384.

On the pelecypod genus *Platopis* Whitfield; III. H. E. VOKES. 137.

Some primitive fossil pelecypods and their possible significance. H. E. VOKES. 233.

The development of the hinge of *Veniella conradi* (Morton) and some conclusions based on its study. H. E. VOKES. 36.

Two new crinoid species from the Henryhouse of Oklahoma. HARRELL L. STRIMPLE. 280.

Physics. Advantages and disadvantages of various interpretations of the quantum theory. HENRY MARGENAU. 265.

Mesons and nuclear forces. HANS A. BETHE. 97.

On research and education—in fluid dynamics. RAYMOND J. SEEGER. 1.

Some newly solved and some unsolved problems in optics. A. I. MAHAN. 165.

Taxonomy. For and against the doctrine of prescription as applied to taxonomy: A historical retrospect. AUSTIN H. CLARK. 13.

Zoology. A new species of the genus *Diarthrodes* (Crustacea, Copepoda) parasitic in a red alga. WOLF-HENRICH FAHRENBACH. 326.

Description of *Eocyzicus concavus* (Mackin) with a review of other North American species of the genus (Crustacea: Conchostraca). N. T. MATTOX. 46.

Fresh-water Ostracoda from Texas and Mexico. WILLIS L. TRESSLER. 138.

Further studies on American millipeds of the family Euryuridae (Polydesmida). RICHARD L. HOFFMAN. 49.

Geographical distribution and means of dispersal of the bathypelagic nemerteans found in the great submarine canyon at Monterey Bay, California. WESLEY R. COE. 324.

New names for two genera of Octocorallia. FREDERICK M. BAYER. 296.

New species of polychaetous worms from the Marianas and Gilbert Islands. OLGA HARTMAN. 228.

Observations on the feeding of prostigmatid larvae (Acarina: Trombidiformes) on arthropods. G. W. WHARTON. 244.

On *Polyclinum indicum*, a new ascidian from the Madras coast of India. V. O. SEBASTIAN. 18.

Two new subterranean shrimps (Decapoda: Caridea) from Florida and the West Indies, with a revised key to the American species. FENNER A. CHACE, Jr. 318.

Zoological contributions of the Lewis and Clark expedition. HENRY W. SETZER. 356.

V
4
1
2
D
E
C
1
9
4
5
XU